

“Cephalaspidean” Heterobranchs (Gastropoda) from the Pacific Coast of Costa Rica

Ángel Valdés¹ and Yolanda E. Camacho-García²

¹ *Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA; Email: avaldes@nhm.org;* ² *Department of Invertebrate Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco, California. 94103, USA; Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, San José, Costa Rica; Email: ycamachogarcia@calacademy.org*

Based on phylogenetic evidence, Mikkelsen (1996) demonstrated that the traditional taxon “Cephalaspidea” is paraphyletic. As a consequence of this new phylogenetic hypothesis, the Acteonidae, Bullinidae, and Ringiculidae were removed from the traditional Cephalaspidea. Furthermore, the Acteonidae was removed from the Opisthobranchia and included in an unresolved group named “Lower Heterobranchia.” The Bullinidae and Ringiculidae remained in the Opisthobranchia, but were included in another unresolved group, the “Architectibranchia.” After the exclusion of these taxa, the rest of the Cephalaspidea remained as a monophyletic group. Members of the paraphyletic traditional Cephalaspidea are here referred to as “cephalaspidean” heterobranchs. Despite the fact that “cephalaspidean” heterobranchs are paraphyletic, it is still practical to deal with them in monographic treatises due to morphological similarities (presence of large, external shells in most groups), shared habitats and life modes, and consistency with historical treatments.

Little is known about the “cephalaspidean” heterobranch biodiversity in Costa Rica. Studies by Houbbrick (1968), Robinson and Montoya (1987), Høisæter, (1998), and more recently by Espinosa and Ortea (2001), provided a few records from the Caribbean and Pacific coast, but included no morphological comparisons for most taxa.

The purpose of the present study is to provide an up-to-date catalogue of species of “Lower Heterobranchia,” “Architectibranchia,” and Cephalaspidea found along the Pacific coast of Costa Rica, including descriptions of a new species and a systematic review of the generic placement and synonymy of several other species previously described, based on new anatomical evidence.

MATERIAL AND METHODS

All specimens studied, including the type material, are deposited at the Instituto Nacional de Biodiversidad, Costa Rica (abbreviated INB), the Natural History Museum of Los Angeles County (abbreviated LACM), the California Academy of Sciences, San Francisco (abbreviated CASIZ), The Natural History Museum, London (abbreviated BMNH), and the National Museum of Natural History, Washington D.C. (abbreviated USNM). The material examined is labeled as “shell” for dried shells (with or without remaining tissue), and “specimen” for complete wet specimens including shell and soft parts. Taxa have been arranged according to a classification system based on the phylogenetic hypothesis by Mikkelsen (1996).

All wet specimens available were dissected and morphological examination was facilitated by

breaking the shell. The internal features were examined and drawn using a dissecting microscope with a camera lucida. Dried shells with remaining tissue were re-hydrated and broken to dissect the radula and other hard parts. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination with a Scanning Electron Microscope (SEM). Gizzard plates were dissected and mounted for examination with a SEM.

SPECIES DESCRIPTIONS

“Lower Heterobranchia”

Family Acteonidae d’Orbigny, 1843

Genus *Acteon* de Monfort, 1810

Acteon traskii Stearns, 1897

(Figs. 1A–D)

Acteon traskii Stearns, 1897:14.

TYPE MATERIAL.— *Acteon traskii*: HOLOTYPE: Spanish Bight, San Diego, California (USNM 2506).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 1 shell (CASIZ 170722). 1 mile offshore, between Bahía Elena and Bahía San Juanillo (10°57’20”N, 85°46’08”W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-12.43). From 1.75 miles west of Punta Descarte to 1.25 miles north of start, off Bahía Santa Elena (11°02’23”N, 85°48’05”W), Provincia Guanacaste, 55 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-15.15). 5 miles north west of Islas Huevos (10°41’45”N, 85°46’25”W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-34.25). Middle of Bahía Huevos, north of Bahía Culebra (10°38’41”N, 85°41’55”W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-35.39). Off beach at Bahía Ballena (9°44’12”N, 84°59’32”W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-45.37). Off Bahía Herradura (9°38’50”N, 84°40’50”W), Provincia Puntarenas, 37 m depth, 10 March 1972, 1 juvenile shell, leg. J. McLean (LACM 72-54.50). Isla David (10°57’51.5100N, 85°42’36.9080W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 39 m depth, 2 March 1996, 3 shells, leg. Y. Camacho (INB0003747064). Isla David (10°58’05.5000N, 85°42’38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 1 shell, leg. Y. Camacho (INB0003747061). 800 meters from Isla Despena, Murciélago (10°59’45.3350N, 85°44’16.2441W), Provincia Guanacaste, 40 m depth, 9 April 2002, 1 shell, leg. F. González (INB0003539758).

ADDITIONAL MATERIAL EXAMINED.— MEXICO: Bahía Chamela, Jalisco, 27–72 m depth, 1 shell, 16 February 1938, leg. G. Willett (LACM 153410). Bahía Tangola-Tangola and Bahía Santa Cruz (15°45’00”N, 96°06’12”W), Oaxaca, 18–37 m depth, 28 February 1934, 2 shells with body parts (LACM 34-133.26). COLOMBIA: Bahía Choco (3°33’N, 77°38–39’W), southwest of Buenaventura, 80 m depth, 16 September 1966, 1 shell (LACM 66-201.8).

SHELL MORPHOLOGY.— Length 12 mm; width 5 mm, in the largest specimen examined from Costa Rica. Shell solid, elongate, with convex sides (Fig. 1A). Body whorl large, from $\frac{1}{4}$ to $\frac{1}{2}$ of the shell length. Spire short, conical, with 3–4 short whorls. Suture slightly channeled. Protoconch globose, about 1.5 whorl, 500 μ m in diameter (Fig. 1B). Umbilicus absent. Aperture long, about $\frac{3}{4}$ of the body whorl length, wide anteriorly, narrowing abruptly about its half-length. Anterior end of the aperture expanded into a small lip that is more conspicuous near the middle of the shell. Columellar margin thickened, slightly oblique, with a small, simple fold. Sculpture composed of a

number of punctured spiral grooves (Fig. 1D). Punctuations oval, fused to each other within each groove, more conspicuous near the anterior end of the shell. Grooves separated by gaps several times as wide as the grooves. Color cream to reddish, with a white band on the posterior end of the whorl. Some specimens with the reddish pigment faded out or completely disappeared.

ANATOMY.— Radular formula $121 \times 133.0.133$ in a specimen from Mexico (LACM 34-133.26). Radular teeth all similar in shape and size, with an elongate base and a curved cusp bearing 15–17 elongate denticles (Fig. 1C).

GEOGRAPHIC RANGE.— Recorded from Southern California to Panama (Keen 1971). The present paper includes the first record from Colombia.

REMARKS.— *Acteon traskii* was described based on Holocene material from southern California (Stearns 1897). Living animals have been reported from southern California to Panama (Keen 1971) and Marcus (1972) provided descriptions of the radula and penial anatomy. This species can be distinguished from *Rictaxis punctocaelatus* (Carpenter, 1864) by having a more fragile, reddish shell with a single white band on the posterior end of the whorl. In *R. punctocaelatus* the shell is dark grey to black with three white bands on the anterior end, middle region, and posterior end of the whorl. The radula of *R. punctocaelatus* described by Marcus (1972) contains a much smaller number of teeth, which are larger and vary in shape along the half-row, from short multidenticulate inner teeth to very elongate outer teeth.

Gosliner (1996) studied one specimen from the Santa Barbara Basin (Southern California) with the shell and radular morphology identical to the specimens here examined. It is most likely that Gosliner's material belongs to the same species.

Acteon panamensis Dall, 1908 is a much shorter and fragile species originally described from deep waters in Panama (Dall 1908).

Rudman (1971) proposed that *Acteon* should be used only for species with a columellar fold and numerous minute hook-shaped teeth. Other genus names are available for species with no columellar fold or radulae with a reduced number of teeth. The anatomy of numerous species and genera of Acteonidae has not been described, so it is not possible to determine their generic placement or synonymy.

Acteon traskii is placed in the genus *Acteon* because of the presence of a wide radula with numerous short teeth, similar to that of *Acteon tornatilis* (Linnaeus, 1758), the type species of the genus. For a description of the radula of *A. tornatilis* see Thompson (1976).

Genus *Crenilabium* Cossmann, 1889

Crenilabium venustus (d'Orbigny, 1840)

(Figs. 1E–G)

Acteon venustus d'Orbigny, 1840:399, pl. 56, figs. 4–6.

? *Daphnella casta* Hinds, 1844:25.

TYPE MATERIAL.— *Acteon venustus*: type material untraceable. *Daphnella casta*: HOLOTYPE: Golfo de Nicoya, Costa Rica (BMNH 79.2.26.89).

MATERIAL EXAMINED.— Five miles north west of Islas Huevos ($10^{\circ}41'45''\text{N}$, $85^{\circ}46'25''\text{W}$), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 3 shells, 1 fragment, leg. P. LaFollette and D. Cadien (LACM 72-34.26). South of Punta Uvita to Isla Ballena ($9^{\circ}07'36''\text{N}$, $83^{\circ}44'30''\text{W}$), Provincia Puntarenas, 18 m depth, 13 March 1972, 1 fragment, leg. J. McLean (LACM 72-61.22).

ADDITIONAL MATERIAL.— Intertidal drift shells in crab colony, Fort Amador Beach ($8^{\circ}56'\text{N}$, $79^{\circ}33'\text{W}$), Canal Zone, Panama, 14 March 1970, 1 shell, leg. A. Marti (LACM 70-85.1).

SHELL MORPHOLOGY.— Length up to 12 mm; width up to 4 mm in the largest specimen exam-

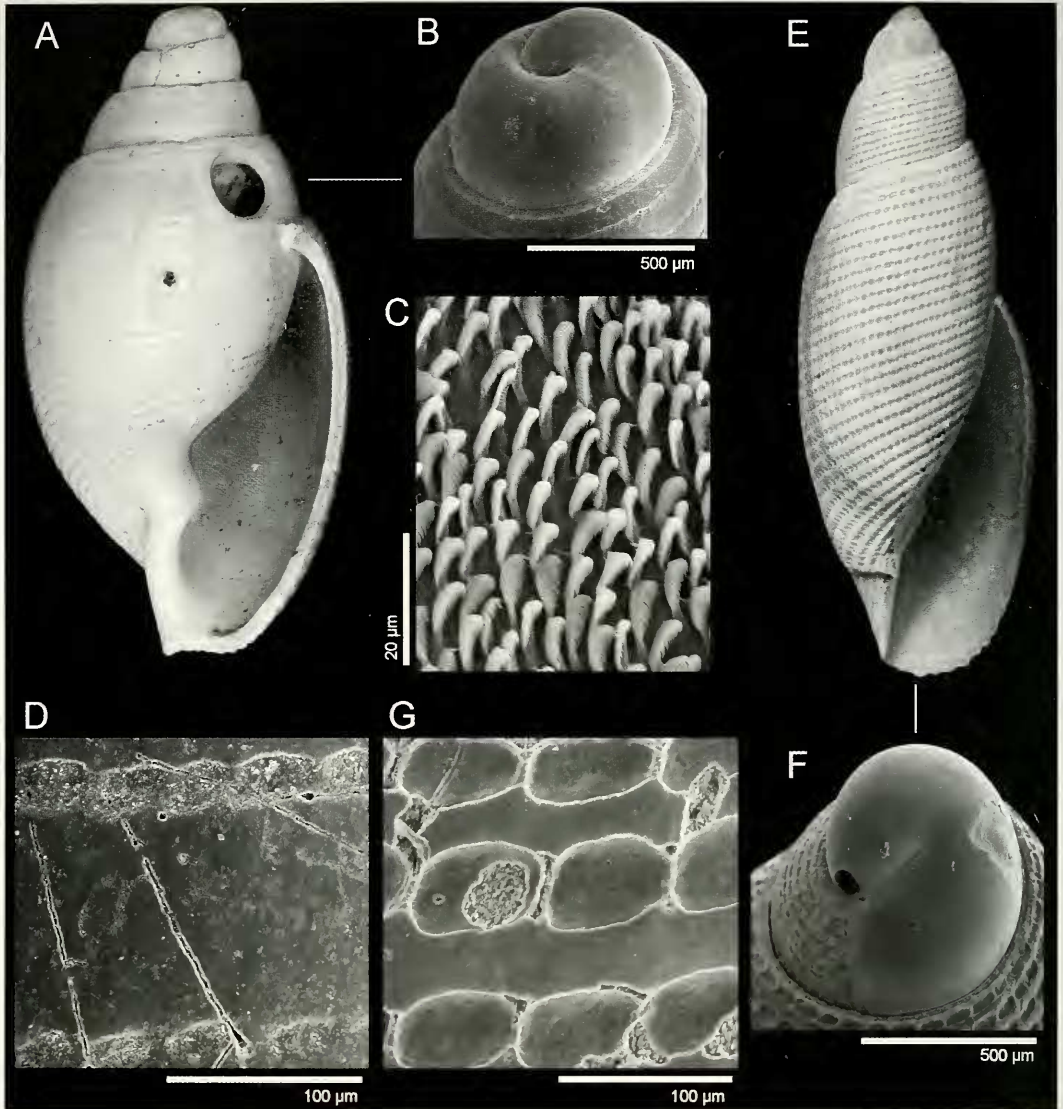


FIGURE 1. A-D, *Acteon traski* Stearns, 1897; (A) Shell morphology, specimen from Isla Despensia (INB0003539758), 6 mm long; (B) Protoconch, specimen from Isla David (INB0003747061); (C) Radular teeth, specimen from Bahia Tangola-Tangola, Mexico (LACM 34-133.26); (D) Sculpture, specimen from Isla David (INB0003747061). E-G, *Crenilabium venustum* (d'Orbigny, 1840); (E) Shell morphology, specimen from Amador Beach, Panama (LACM 70-85.1), 9 mm long; (F) Protoconch, specimen from Punta Uvita (LACM 72-61.22); (G) Sculpture, same specimen.

ined. Shell solid, very elongate (Fig. 1E). Body whorl long, between $\frac{1}{5}$ – $\frac{2}{5}$ of the shell length; spire conical, elongate, with 2–3 whorls. Suture narrowly channeled. Protoconch elongate, about 1.5 whorl, 600 μ m in diameter (Fig. 1F). Umbilicus absent. Aperture narrow and short, about $\frac{3}{4}$ of the body whorl. Columellar margin with a conspicuous denticle. Sculpture composed of a number of punctured spiral grooves (Fig. 1G). Punctuations conspicuous, oval, situated next to each other within each groove. Grooves separated by gaps with about the same width as the grooves. Color uniformly whitish.

ANATOMY.— All the specimens examined consisted of empty shell so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— Reported from Costa Rica to Peru (Keen 1971).

REMARKS.— *Acteon venustus* d'Orbigny, 1840 was originally described from Paita, Peru (d'Orbigny 1840). This species is characterized by having a narrow and elongate shell, with an elongate spire, a relatively short aperture, and a strong sculpture composed of conspicuous punctuations. There is no information on the anatomy of this species that was described on the basis of empty shells. The material here examined from Costa Rica and Panama matches the original description and it is clear that it belongs to the same species.

Because there are no anatomical data, it is not possible to provide a positive taxonomic placement for this species. Bouchet (1975) provided anatomical and conchological evidence for maintaining the fossil genus *Crenilabrum* as valid, those include a radula with lateral teeth provided with a long and sharp cusp and a rachidian tooth, and a shell with a very elongate spire and comparatively short aperture. The type material of *Acteon venustus*, as well as the specimens here examined, resembles the conchological features of *Crenilabrum*. Thus, this species is here tentatively transferred to *Crenilabrum* until complete specimens become available for study.

Daphnella castus (Hinds, 1844) was originally described as a member of the Turridae, and later transferred to *Acteon* by Keen (1971). The holotype of this species (BMNH 79.2.26.89) is partially broken, but the general outline of the shell is very similar to that of *Crenilabrum venustus* and these two names are most likely synonyms.

Genus *Rictaxis* Dall, 1871

Rictaxis punctocaelatus (Carpenter, 1864)

Tornatella punctocaelata Carpenter, 1864:646.

Remarks.— This species has been reported in the literature from Alaska to Baja California (Keen 1971; Skoglund 2002). The LACM collection holds one lot containing two shells collected alive from Isla San Miguel, Panama (LACM 157893). No specimens have been collected so far from Costa Rica but it is likely that this species is present in this area.

Rictaxis punctocaelatus is characterized by having a solid and elongate shell with a black or dark gray background color and three spiral white bands on the anterior and posterior ends of the spire as well as in the middle region. The radula and external morphology of this species was described by Gosliner (1996).

Opisthobranchia

Cephalaspidea

Family Cylichnidae H. and A. Adams, 1854

Genus *Cylichna* Lovén, 1846

Cylichna atahualpa (Dall, 1908)

(Figs. 2A–C)

Cylichnella atahualpa Dall, 1908:243, pl. 11, fig. 2.

TYPE MATERIAL.— *Cylichnella atahualpa*: HOLOTYPE: Gulf of Panama (USNM 123081).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 1 shell (CASIZ 170721). Bahía Chatham (5°33'20"N, 86°59'10"W), Cocos Island, 26 m depth, 13 January 1938, 11

shells (LACM 38-179.4). Golfo Dulce (8°24'20"N, 83°13'40"W), Provincia Puntarenas, 35–88 m depth, 26 March 1939, 1 shell (LACM 39-44.23). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 7 shells and fragments, leg. P. LaFollette and D. Cadien (LACM 72-12.45). Half mile to one mile and half west of Roca Vagares, Bahía de San Juanillo (10°57'28"N, 85°45'20"W), Provincia Guanacaste, 37 m depth, 14 February 1972, 2 shells, leg. D. Cadien and P. LaFollette (LACM 72-13.33). Five miles north west of Islas Huevos (10°41'45"N, 85°46'25"W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 10 shells, leg. P. LaFollette and D. Cadien (LACM 72-34.28). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 4 shells, leg. J. McLean (LACM 72-54.52). Off Isla del Caño (8°45'N, 83°54'W), Provincia Puntarenas, 55 m depth, 16–17 March 1972, 6 shells, leg. J. McLean (LACM 72-66.40).

SHELL MORPHOLOGY.—Length up to 12 mm; width up to 3 mm in the largest specimen examined. Shell solid, elongate, with nearly parallel sides (Fig. 2A). Only one whorl visible, forming nearly the entire shell. Apex rounded, umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded, slightly flattened in some specimens. Aperture as long as the shell, wider anteriorly and narrowing gradually at about $\frac{1}{5}$ of its length. Columellar margin conspicuously thickened. Umbilicus absent. Sculpture with a number of irregular spiral lines more conspicuous near the anterior and posterior ends of the shell. Color dirty white, covered with a pale brown or yellowish periostracum. Spiral lines near the anterior and posterior borders of the shell pale brown. Apex and columella opaque white.

ANATOMY.—The digestive system contains three smooth gizzard plates similar in shape and size. All the plates are oval and elongate (Fig. 2C). The radular formula is $12 \times 4.1.1.1.4$ in a specimen from Golfo Dulce (LACM 39-44.23). The rachidian teeth are broad with a number of sharp denticles decreasing in size towards the laterals of each plate. The innermost lateral teeth are hook-shaped, with a long and strong cusp with numerous minute denticles (Fig. 2B). The four outermost teeth of each row are much smaller, but also hook-shaped with a long and thin cusp and several small denticles.

REMARKS.—*Cylichna atahualpa* was described based on shells collected at 590 m depth from the Gulf of Panama (Dall 1908). The original description included an illustration of an elongate shell with no umbilicus and the columellar margin conspicuously thickened. The color of the shell was described as white with a pale yellowish periostracum that shows reddish brown in the incised sculpture. The material here examined is from shallower waters but fits the original description and characteristics of the holotype of *Cylichna atahualpa*.

This species was originally described as a member of *Cylichnella*, but the anatomy of the specimens examined, with three oval and smooth gizzard plates, and a radula with several lateral teeth, are typical of species of *Cylichna*.

Other species assigned to *Cylichna*, also described or reported from the Panamic Province, are *Cylichna luticola* (C.B. Adams, 1852), *Cylichna inca* (Dall, 1908), and *Cylichna pizarro* (Dall, 1908). According to the illustrations provided by Keen (1971), these species are proportionally shorter and wider than *C. atahualpa* and lack conspicuous spiral lines on the shell, except for *C. pizarro*.

Cylichna diegensis (Dall, 1919), originally described from San Diego, California, and with a geographic range extending from Santa Monica to Baja California, has a similar shell morphology to *C. atahualpa*. The anatomy of *C. diegensis* was described by Gosliner (1996), and it differs from that of *C. atahualpa* in several regards. The inner lateral teeth of *C. diegensis* bear 9–11 large denticles under the main cusp, whereas in *C. atahualpa* there are numerous minute denticles. Additionally, the outermost teeth of *C. diegensis* are smooth, whereas in *C. atahualpa* they have numerous denticles.

Genus *Acteocina* Gray, 1847***Acteocina infrequens* (C.B. Adams, 1852)**

(Figs. 2D–H)

Bulla (*Tornatina*) *infrequens* C.B. Adams, 1852:214, 319.*Acteocina magdalenensis* Dall, 1919:296.*Acteocina angustior* Baker and Hanna, 1927:124–125, pl. 4, fig. 5.

TYPE MATERIAL.—*Bulla* (*Tornatina*) *infrequens*: LECTOTYPE: Panama (MCZ 186451). *Acteocina magdalenensis*: HOLOTYPE: Bahía Magdalena, Baja California, Mexico, leg. C. R. Orcutt (USNM 218410). *Acteocina angustior*: HOLOTYPE: Puerto Escondido, Baja California, Mexico (CASIZ 032116).

MATERIAL EXAMINED.—Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 6 shells (CASIZ 170720). Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 31 shells (LACM 33-123.32). Puerto Parker (10°57'50"N, 85°48'45"W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 11 shells (LACM 35-113.27). Bahía Salinas (11°03'33"N, 85°43'47"W), 11 February 1935, 4 shells (LACM 35-117.19). Bahía Salinas (11°03'33"N, 85°44'05"W), 11 February 1935, 1 shell (LACM 35-122.16). Between Punta Isla and 500 m South of Punta Isla (10°56'00"N, 85°48'55"W), Bahía Santa Elena, Provincia Guanacaste, 1–11 m depth, 13 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-7.33). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55'15"N, 85°48'30"W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, >50 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.18). Bahía Potrero Grande (10°50'56"N, 85°48'35"W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 17 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.12). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.44). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.35). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 3 shells, leg. J. McLean (LACM 72-54.56). Isla del Caño (8°44'00"N, 83°52'30"W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 6 shells, leg. J. McLean (LACM 72-64.18). 250 m off Punta Piedra (8°35'24.6720N, 83°11'26.3250W), Provincia Puntarenas, 23 m depth, 14 April 1997, 2 shells, leg. M. Madrigal (INB0001496381). Playa San Miguel (9°34'39.3620N, 85°08'05.5470), Cabo Blanco, Provincia Puntarenas, 0 m depth, 13 November 1995, leg. F. Alvarado (INB0003096615). 1.5 km northwest of Playa Junquillal (10°58'40.7139N, 85°42'27.2867W), Bahía Junquillal, Provincia Guanacaste, 20 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003453953). 200 m northwest of Playa Guaria (10°57'55.1620N, 85°42'23.7922W), Bahía Junquillal, Provincia Guanacaste, 8 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003458479). Between Isla Bolaños and Playa Coyotera (11°02'51.0971N, 85°43'21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 10 April 2002, 3 shells, leg. F. González (INB0003502789). 1.5 km west of Puerto Soley (11°02'35.2251N, 85°41'47.9633W), Bahía Salinas, 10 m depth, 10 April 2002, 8 shells, leg. F. González (INB0003503459). 1 km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 5 April 2002, 17 shells, leg. F. González (INB0003503569). 400 m west of Isla Cabo Blanco (9°32'29.2960N, 85°07'16.0340W), Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 16 May 1998, 14 shells, leg. A. Berrocal (INB0003539964). Between Punta Piedra and Punta Gallardo (8°35'47.5010N, 83°11'58.9990W), Provincia Puntarenas, 30–35 m depth, 13 June 1997, 12 shells, leg. M. Madrigal (INB0003542480). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 11 shells, leg. S. Ávila (INB0003575679). Playa Ballena (9°06'34.2870N, 83°41'46.4390W), Provincia Puntarenas, 1 m depth, 16 April 1996, 1 shell, leg. Y. Camacho (INB0003722811). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 2 shells, leg. Y. Camacho (INB0003722813).

SHELL MORPHOLOGY.—Length up to 9 mm; width up to 3.5 mm in the largest specimen examined. Shell solid, elongate, fusiform, with almost parallel sides (Fig. 2D–E). Body whorl very

large; spire long and conical in some specimens (Fig. 2E) or short and compressed in others (Fig. 2D), with 2–3 whorls. Suture canaliculated. Protoconch flattened, about 1.5 whorls, 300 μm in diameter (Fig. 2F), attached to the teleoconch by the aperture. Umbilicus absent. Aperture very long, about $\frac{7}{10}$ of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a long, thin callus running from its anterior end to about $\frac{1}{5}$ – $\frac{1}{2}$ of the aperture length. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

ANATOMY.— Digestive system containing three smooth and irregular gizzard plates, all of them similar in shape and size (Fig. 2G). Radular formula $16 \times 1.0.1$ in a specimen from Bahía Potrero Grande (LACM 72-29.12). Lateral teeth hook-shaped with a number of small denticles on the single, curved cusp (Fig. 2H).

GEOGRAPHIC RANGE.— Recorded from Baja California to Panama (Keen 1971).

REMARKS.— Marcus (1977) considered that *Acteon wetherillii* Lea, 1833, the fossil type species of *Acteocina*, is either a member of the Retusidae or Cylichnidae, but different from the common usage of the name *Acteocina* by modern authors. Marcus (1977) was unable to determine the position of this species, so she decided to use the next available name for this genus, which is *Tornatina* A. Adams, 1850. Marcus (1977) also maintained *Utriculastra* as different from *Acteocina* because of anatomical differences in the number of denticles on the radular teeth and the position of the esophagus.

On the contrary, Mikkelsen and Mikkelsen (1984) commented that *Acteon wetherillii* is a synonym of the recent species *Acteocina canaliculata* (Say, 1826), and therefore the name *Acteocina* should be maintained as valid. A comparison of the original descriptions of *A. wetherillii* (Lea 1833) and the redescription of *A. canaliculata* by Mikkelsen and Mikkelsen (1984) revealed that their shell morphology is in fact very similar. Mikkelsen and Mikkelsen (1984) also added *Utriculastra* Thiele, 1925 and *Cylichnella* Gabb, 1873 to the synonymy of *Acteocina*, following Gosliner (1979) who regarded *Utriculastra* and *Cylichnella* as synonyms. *Utriculastra* was originally based on *A. canaliculata* (the type species by original designation), and, therefore, it is an objective synonym of *Acteocina*. However, *Cylichnella* differs considerably from *Acteocina* in shell morphology. Gosliner (1979) commented that *Cylichnella* has an involute spire whereas *Utriculastra* possesses a projecting apex. Despite these differences, he regarded these two genera as synonyms because of a similar anatomy.

Due to the remarkable differences in shell morphology between *Cylichnella* and *Acteocina*, these two genera are here maintained as distinct. Marcus (1977) and Mikkelsen and Mikkelsen (1984) revised several species of *Acteocina* and provided detailed anatomical descriptions. The diagnosis above is based on these two papers.

Adams (1852) described *Bulla infrequens* based on two shells collected from Panama. The shells were not illustrated and described as being cylindrical, with a long aperture having a thick columellar plait, a moderately elevated, deeply channeled spire, and a white and smooth surface.

Dall (1919) described *Acteocina magdalenensis* from Bahía Magdalena, Baja California Sur, Mexico, with similar characteristics to those of *Acteocina infrequens*. Examination of the holotype (USNM 218410) reveals no substantial differences with the lectotype of *A. magdalenensis* and therefore these two names are regarded as synonyms.

A second synonym is *Acteocina angustior* described by Baker and Hanna (1927) from Puerto Escondido, Baja California, Mexico. The description and features of the holotype (CASIZ 032116) are undistinguishable from those of *Acteocina infrequens*. Baker and Hanna (1927) compared *A. angustior* with *Acteocina culcitella* Gould, 1852 (a northern species), but not with other Panamic species.

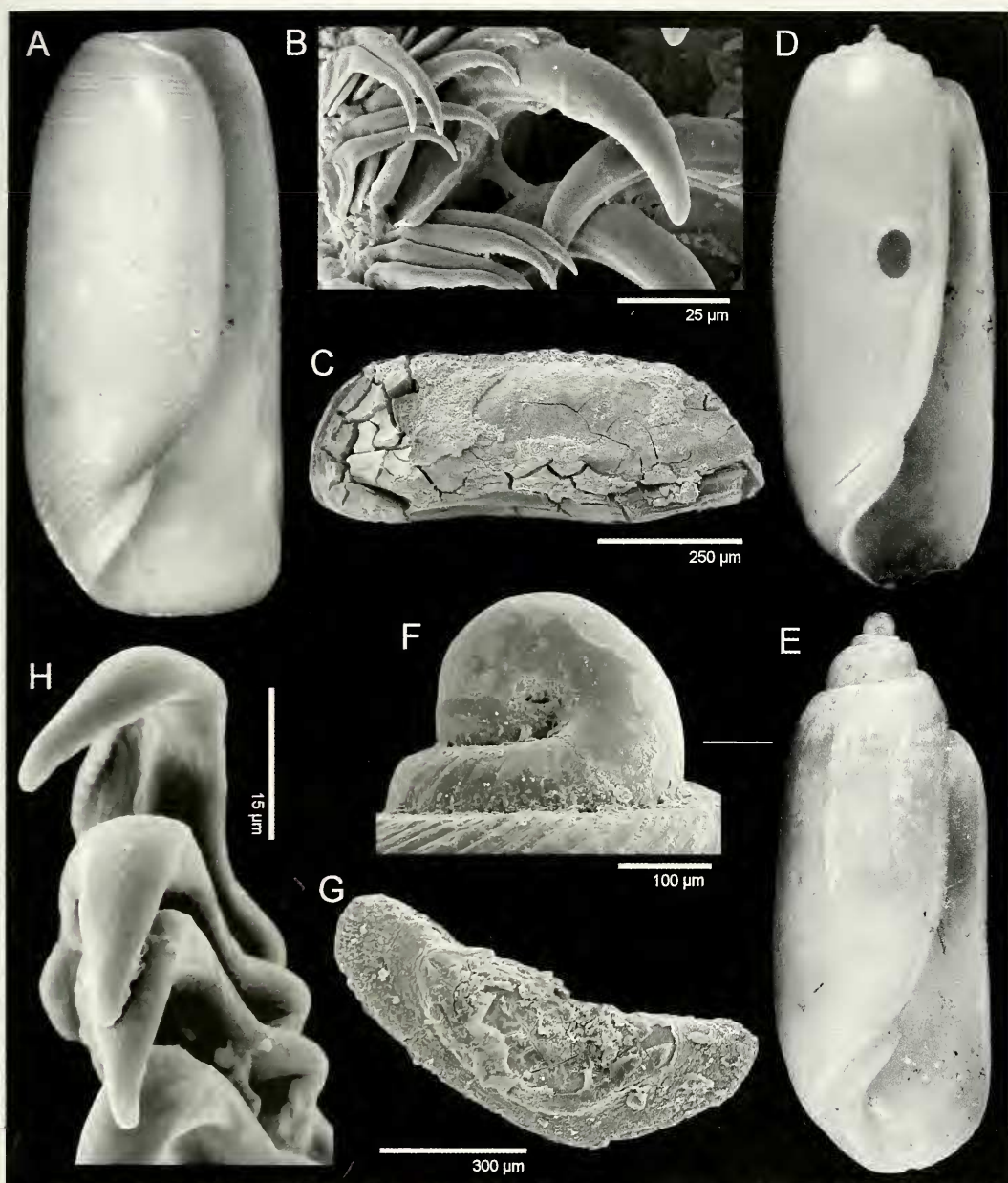


FIGURE 2. A–C, *Cylichna atahualpa* (Dall, 1908); (A) Shell morphology, specimen from Golfo Dulce (LACM 39-44.23), 6.5 mm long; (B) Radular teeth, specimen from Golfo Dulce (LACM 39-44.23); (C) Gizzard plate, same specimen. D–H, *Acteocina infrequens* (C.B. Adams, 1852); (D) Shell morphology, specimen from Isla Cabo Blanco (INB0003539964), 8 mm long; (E) Shell morphology, specimen from Bahía Cuajiniquil (INB0003575679), 4 mm long; (F) Protoconch, specimen from Playa Junquillal (INB0003503569); (G) Gizzard plate, specimen from Bahía Potrero Grande (LACM 72-29.12); (H) Radular teeth, same specimen.

Acteocina carinata (Carpenter, 1857)

(Figs. 3A–C)

Tornatina carinata Carpenter, 1857:171.**TYPE MATERIAL.**— *Tornatina carinata*: SYNTYPES (6): Mazatlán, Mexico (BMNH).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 25 shells (CASIZ 170719). Puerto Culebra (10°35'N, 85°40'W), Provincia Guanacaste, 31 m depth, 13 March 1934, 1 shell (LACM 33-153.10). Puerto Culebra, (10°37'N, 85°40'W), Provincia Guanacaste, 27 m depth, 26 February 1934, 2 shells (LACM 34-253.5). Playa Blanca, Bahía Playa Blanca, Provincia Guanacaste (10°56'45"N, 85°53'30"W), 3–5 m depth, 8 February 1935, 3 shells (LACM 35-100.7). Puerto Parker (10°57'50"N, 85°48'45"W), Golfo Santa Elena, 55 m depth, 9 February 1935, 2 shells (LACM 35-113.24). Bahía Salinas (11°03'33"N, 85°43'47"W), 11 February 1935, 3 shells (LACM 35-117.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo, (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 15 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.44). Half mile to one mile and half west of Roca Vagares, Bahía de San Juanillo (10°57'28"N, 85°45'20"W), Provincia Guanacaste, 37 m depth, 14 February 1972, 1 shell, leg. D. Cadien and P. LaFollette (LACM 72-13.32). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02'22"N, 85°45'16"W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.43). Bahía Potrero Grande (10°50'56"N, 85°48'35"W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 7 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.10). Five miles north west of Islas Huevos (10°41'45"N, 85°46'25"W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34.27). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 6 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.40). Half mile off mouth of Bahía Huevos (10°38'22"N, 85°42'52"W), Provincia Guanacaste, 36–42 m depth, 19 February 1972, 7 shells, leg. P. LaFollette and D. Cadien (LACM 72-36.24). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 18 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.30). Anchorage at Bahía Ballena off Tambor (10°44'10"N, 84°59'34"W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 1 shell, leg. P. LaFollette and A. Ferreira (LACM 72-43.17). Off beach at Bahía Ballena (9°44'12"N, 84°59'32"W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.38). Islet and rocks 1 km west of Isla Alcatraz (9°47'N, 84°53.5'W), Islas Tortugas, Provincia Puntarenas, 2–8 m depth, 23–24 February 1972, 1 shell, leg. P. LaFollette, D. Cadien, and A. Ferreira (LACM 72-46.58). Bahía Herradura (9°37'58"N, 84°40'30"W), Provincia Puntarenas, 21 m depth, 9 March 1972, 13 shells, leg. J. McLean (LACM 72-53.29). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 27 shells, leg. J. McLean (LACM 72-54.51). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.38). Small islets of Quepos (9°22'12"N, 84°09'15"W), Provincia Puntarenas, 23 m depth, 12 March 1972, 5 shells, leg. J. McLean (LACM 72-59.30). South of Punta Uvita to Isla Ballena (9°07'36"N, 83°44'30"W), Provincia Puntarenas, 18 m depth, 13 March 1972, 1 fragment, leg. J. McLean (LACM 72-61.23). Off Isla del Caño (8°45'N, 83°54'W), Provincia Puntarenas, 55 m depth, 16–17 March 1972, 1 shell, leg. J. McLean (LACM 72-66.39). From Punta Piedra to Punta Gallardo (8°35'47.5010N, 83°11'58.9990W), Golfo Dulce, Provincia Puntarenas, 35 m depth, 13 June 1997, 1 shell, leg. M. Madrigal (INB0001496191). Playa San Miguel (9°34'39.3620N, 85°08'05.5470W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 13 November 1995, 7 shells, leg. F. Alvarado (INB0003096504). 1.5 km northwest of Playa Junquillal (10°58'40.7139N, 85°42'27.2867W), Santa Rosa, Provincia Guanacaste, 20 m depth, 4 April 2002, 6 shells, leg. F. González (INB0003501408). Playa Naranjo (10°48'16.0960N, 85°41'12.0680W), Estero Real, Provincia Guanacaste, 0 m depth, 6 March 1995, 1 shell, leg. S. Ávila (INB0003539800). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 5 shells, leg. Y. Camacho (INB0003542874). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 5 shells, leg. Y. Camacho (INB0003542915). Isla David (10°56'32.2000N, 85°42'51.1000), Santa Rosa, Provincia

Guanacaste, 18 m depth, 4 shells, 12 March 1996, leg. Y. Camacho (INB0003575624). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 21 shells, leg. Y. Camacho (INB0003575670). 1 km east of Punta Cirial (9°56'10.2222N, 84°52'43.1248W), Isla San Lucas, Provincia Puntarenas, 22.6 m depth, 9 December 1999, 1 shell, leg. M. Calderón (INB0003722804). 400 m west of Isla Cabo Blanco (9°32'29.2960N, 85°07'16.0340W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 16 May 1998, 6 shells, leg. A. Berrocal (INB0003722806). Golfo de Papagayo (10°22'00.0000N, 86°15'00.0000W), 100 m depth, 10 February 1995, 2 shells, leg. Y. Camacho (INB0003722814). Dock of Playa San Miguel (9°34'36.9190N, 85°08'06.3610W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 2 May 1995, 4 shells, leg. G. Mena (INB0003722818). Punta Oliva (9°34'39.3370N, 85°08'15.3840W), Cabo Blanco, Provincia Puntarenas, 0 m depth, 16 September 1995, 4 shells, leg. F. Alvarado (INB0003722821). La Viuda Rock (8°36'56.0065N, 83°14'08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722824). Golfo Santa Elena (10°58'45.4310N, 85°43'01.8500W), Bahía Junquillal, Provincia Guanacaste, 0–3 m depth, 13 March, 1996, 31 shells, leg. R. Angulo (INB0003722830). Boca de Estero Bocón (8°32'57.0600N, 83°18'51.2380W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 13 June 1995, 1 shell, leg. M. Lobo (INB0003747047). La Viuda Rock (8°36'56.0065N, 83°14'08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 23 shells, leg. M. Lobo (INB0003747054).

SHELL MORPHOLOGY.— Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with almost parallel sides (Fig. 3A–B). Body whorl very large; spire short, with 3 whorls, flattened in some specimens (Fig. 3A) and conical in others (Fig. 3B). Suture not channeled. Posterior end of the whorls with an ornated sharp ridge (carina) with longitudinal bands. Protoconch flattened, about 1.2 whorls, 200 μ m in diameter (Fig. 3C). It is only attached to the teleoconch by the aperture. Umbilicus absent. Aperture very long, between $\frac{7}{10}$ and $\frac{9}{10}$ of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a thin callus running from its anterior end to about $\frac{1}{5}$ – $\frac{1}{7}$ of the aperture length. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— Known from the Gulf of California to Costa Rica (Keen 1971).

REMARKS.— Carpenter (1857) described this species as different from *Acteocina infrequens* by having a more irregular spire, a suture not channeled and a shoulder sharply carinated. Additionally, the shell of *A. infrequens* is elongate, with the end of the whorls rounded and the protoconch is about 300 μ m in diameter, whereas the shell of *Acteocina carinata* has the posterior end of the whorls with a sharp ridge ornated with longitudinal bands and the protoconch is about 200 μ m in diameter.

Acteocina harpa (Dall, 1871), originally described from California by Dall (1871) has a shell morphology similar to that of *A. carinata*, but according to Gosliner (1996), the former differs by having more asymmetrical gizzard plates and a rachidian tooth with fewer denticles.

Acteocina sp. 1

(Figs. 3D–E)

MATERIAL EXAMINED.— 0.9 mile off beach at Bahía Potrero (10°27'42"N, 85°48'15"W), Provincia Guanacaste, 16–18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-39.13). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-40.31).

SHELL MORPHOLOGY.— Length up to 4.5 mm; width up to 2.5 mm in the largest specimen examined. Shell fragile, oval, with a convex right side and concave left side (Fig. 3D). Body whorl

very large; spire short and conical, with 1–2 whorls. Suture canaliculated. Protoconch flattened, about 1.5 whorls, 150 μm in diameter (Fig. 3E). Umbilicus absent. Aperture very long, about $\frac{1}{5}$ of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a long, thick callus. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

ANATOMY.— All the specimens examined consisted of empty shells, so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— This species is only known from Costa Rica (present paper).

REMARKS.— This appears to be a distinct species of *Acteocina*, but it is not described herein because of the absence of anatomical data.

Acteocina sp. 1 is easily distinguishable from both *Acteocina infrequens* and *Acteocina carinata* by its shell morphology. The shell of *Acteocina* sp. 1 is shorter, more oval than that of *A. infrequens* and most specimens of *A. carinata*. In addition, the spire of *Acteocina* sp. 1 is shorter than in the other two species and the posterior end of the whorl lacks the sharp ridge ornated with longitudinal bands of *A. carinata*. The protoconch of *Acteocina* sp. 1 is considerably smaller than in the other two species.

Acteocina sp. 2

(Figs. 3F–G)

MATERIAL EXAMINED.— Puerto Jiménez (8°32.5'N, 83°19.5'W), Golfo Dulce, Provincia Puntarenas, 20 March, 1972, 1 shell, leg. J. McLean (LACM 72-69.17). Bahía El Hachal (10°56'08.9540N, 85°43'58.7890W), Provincia Guanacaste, 0 m depth, 15 September 1994, 2 shells, leg. C. Cano (INB0001480928). Boca de Estero Caballero (8°40'06.3050N, 83°26'41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 11 shells, leg. M. Lobo (INB0001499798). Quebrada Palma (8°39'06.8780N, 83°26'10.8200W), Playa Blanca, Golfo Dulce, Provincia Puntarenas, 0 m depth, 7 April 1995, >50 shells, leg. G. Mena (INB0003537637). Boca de Estero Caballero (8°40'06.3050N, 83°26'41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 11 shells, leg. M. Lobo (INB0003540727). Punta Palma (8°38'59.5510N, 83°26'07.5540W), Golfo Dulce, Provincia Puntarenas, 2 m depth, 12 June 1995, 7 shells, leg. M. Lobo (INB0003722822). 1 km south of Puntarenitas (8°36'55.7150N, 83°10'07.7110W), Provincia Puntarenas, 0 m depth, 13 May 1997, 1 shell, leg. S. Ávila (INB0003726899). Punta Palma (8°38'59.5510N, 83°26'07.5540W), Golfo Dulce, Provincia Puntarenas, 2 m depth, 12 June 1995, 31 shells, leg. M. Lobo (INB0003747326). Boca de Estero Bocón (8°32'57.0600N, 83°18'51.2380W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 13 June 1995, 7 shells, leg. M. Lobo (INB0003747047). Sector Playitas (8°44'19.1980N, 83°21'57.0660W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 2 shells, leg. M. Lobo (INB0003747549).

SHELL MORPHOLOGY.— Length up to 3 mm; width up to 1.5 mm in the largest specimen examined. Shell fragile, elongate, posteriorly truncate, with almost parallel sides (Fig. 3F). Body whorl very large; spire short, almost flat. Suture canaliculated. Protoconch flattened, partially embedded in the teleoconch, 200 μm in diameter (Fig. 3G). Umbilicus absent. Aperture very long, about $\frac{1}{10}$ of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique. Sculpture with conspicuous spiral lines, more densely arranged near the anterior end of the shell, crossed by faint axial lines. Color uniformly whitish to pale brown.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— This species is only known from several localities in Costa Rica (present paper).

REMARKS.— This appears to be a distinct species of *Acteocina*, but it is not described herein because of the absence of anatomical data.

This species is superficially similar to *Acteocina carinata* in shell morphology, but these two species are easily distinguishable by the presence of a shorter spire in *Acteocina* sp. 2, with the protoconch partially embedded in the teleoconch. Additionally, the sculpture of *Acteocina* sp. 2 has conspicuous spiral lines, more densely arranged near the anterior end of the shell, which are absent in *A. carinata*.

Genus *Cylichnella* Gabb, 1873

Cylichnella tabogaensis (Strong and Hertlein, 1939)

(Figs. 4A–C)

Retusa tabogaensis Strong and Hertlein, 1939:191–192, pl. 18, fig. 4.

TYPE MATERIAL.— *Retusa tabogaensis*: PARATYPE: off Isla Taboga, Panama (LACM 1341).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 9 shells (CASIZ 170717). Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.27). Puerto Culebra (10°35'N, 85°40'W), Provincia Guanacaste, 31 m depth, 13 March 1934, 4 shells (LACM 33-153.11). Playa Blanca (10°56'45"N, 85°56'W), Provincia Guanacaste, 73 m depth, 8 February 1935, 1 shell (LACM 33-103.14). Bahía Salinas (11°03'33"N, 85°43'47"W), 11 February 1935, 2 shells (LACM 35-117.16). Southeast end of Bahía Santa Elena, approximately 0.5 mile offshore (10°55'15"N, 85°48'30"W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 10 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.46). Half mile to one mile and half west of Roca Vagares, Bahía San Juanillo (10°57'28"N, 85°45'20"W), Provincia Guanacaste, 37 m depth, 14 February 1972, 6 shells, leg. D. Cadien and P. LaFollette (LACM 72-13.34). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02'22"N, 85°45'16"W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.44). Five miles north west of Islas Huevos (10°41'45"N, 85°46'25"W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34). 250 m off Punta Piedra (8°35'24.6720N, 83°11'26.3250), Provincia Puntarenas, 23 m depth, 14 April 1997, 8 shells, leg. M. Lobo (INB0001496380). Between Isla Bolaños and Playa Coyotera (11°02'51.0972N, 85°43'21.1040W), Provincia Guanacaste, 12 m depth, 10 April 2002, 1 shell, leg. A. Berrocal (INB0003539773). From 500 m off the beach to 2.5 km south-east (8°34'39.1040N, 83°11'29.6540W), Punta Piedra, Provincia Puntarenas, 14–90 m depth, 10 April 1997, 24 shells, leg. M. Madrigal (INB0003540314). Between Punta Piedra and Punta Gallardo (8°35'47.5010N, 83°11'58.9990W), Golfo Dulce, Provincia Puntarenas, 30–35 m depth, 13 June 1997, 11 shells, leg. M. Madrigal (INB0003540361). 1 Km northwest of Playa Coronado (9°59'54.1430N, 84°58'49.6030W), Isla Caballo, Provincia Puntarenas, 10 m depth, 7 December 1999, 2 shells, M. Calderón (INB0003542209). Isla David (10°56'32.2000N, 85°42'51.1000W), Provincia Guanacaste, 18 m depth, 12 March 1996, 7 shells, leg. Y. Camacho (INB0003575621). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003575666). La Viuda Rock (8°36'56.0065N, 83°14'08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722823). Bahía Junquillal (10°59'13.0310N, 85°43'16.7950W), Golfo Santa Elena, Provincia Guanacaste, 3 m depth, 2 shells, 13 March 1996, leg. R. Angulo (INB0003722827). Golfo Santa Elena (10°58'45.4310N, 85°43'01.8500W), Bahía Junquillal, Provincia Guanacaste, 0–3 m depth, 13 March, 1996, 2 shells, leg. R. Angulo (INB0003722831). 250 m off Punta Piedra (8°35'24.6720N, 83°11'26.3250), Provincia Puntarenas, 23 m depth, 14 April 1997, 14 shells, leg. M. Lobo (INB0003747050). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 11 shells, leg. Y. Camacho (INB0003747059). Playa Mostrencal (10°59'47.3060N, 85°42'53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March

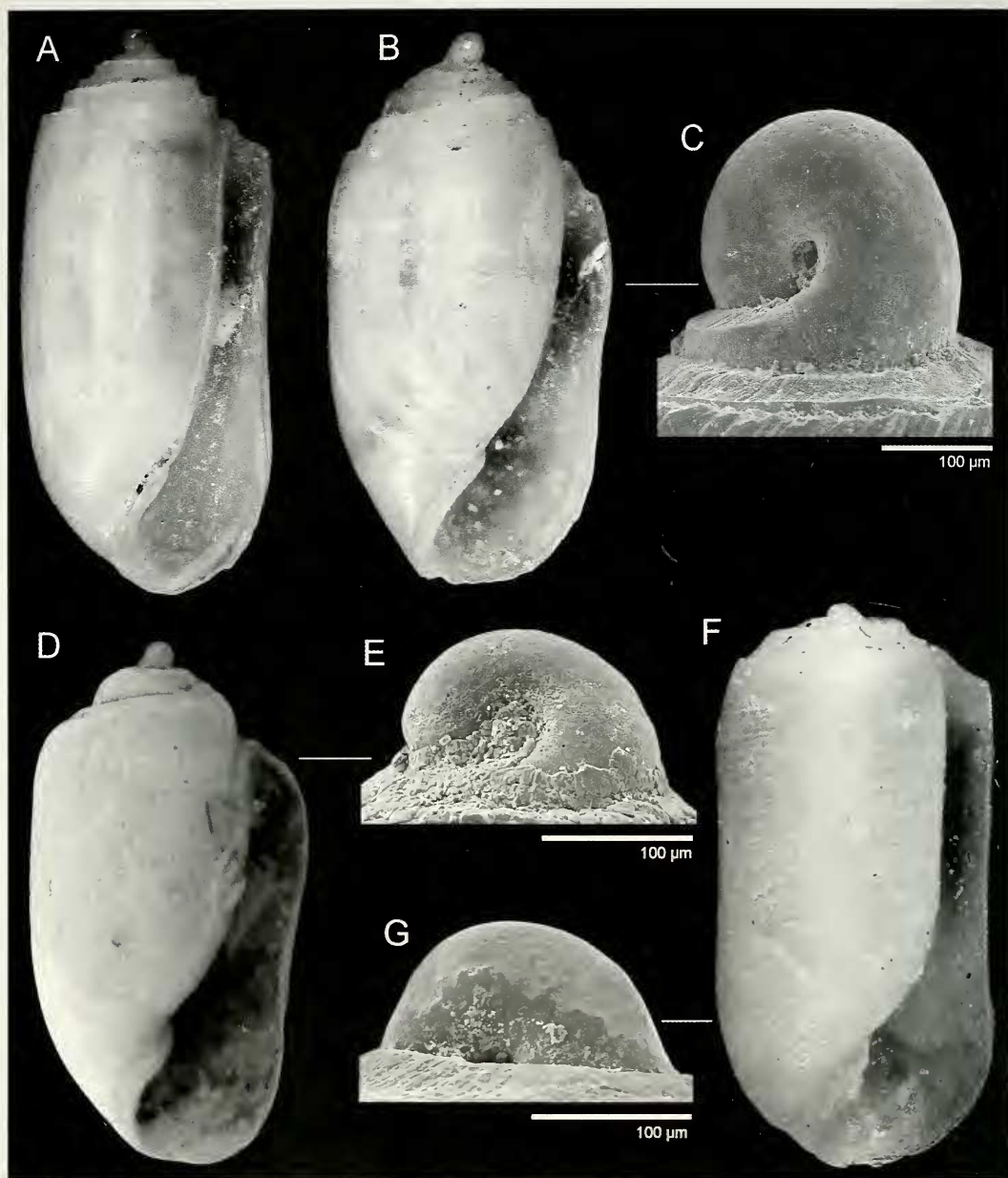


FIGURE 3. A–C, *Acteocina carinata* (Carpenter, 1857); (A) Shell morphology, specimen from Bahía Junquillal (INB0003722830), 4 mm long; (B) Shell morphology, specimen from Isla Cabo Blanco (INB0003722806), 4 mm long (C) Protoconch, specimen from Isla Cabo Blanco (INB0003722806). D–E, *Acteocina* sp. 1; (D) Shell morphology, specimen from Bahía Potrero (LACM 72-40.31), 4 mm long; (E) Protoconch, same specimen. F–G, *Acteocina* sp. 2; (F) Shell morphology, specimen from Golfo Dulce (INB0003747549), 2.5 mm long; (G) Protoconch, specimen from Golfo Dulce (INB0003537637).

1996, leg. R. Angulo (INB0003747411). 1 km east of Punta Cirial (9°56'10.2222N, 84°52'43.1248W), Isla San Lucas, Provincia Puntarenas, 0–22 m depth, 9 December 1999, 1 shell, leg. M. Calderón (INB0003747485).

SHELL MORPHOLOGY.—Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Fig. 4A). Only one whorl visible, forming nearly the entire shell, except for a portion of the top of the spire. Apex rounded, umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly and narrowing gradually at about $\frac{1}{4}$ of its length. Columellar margin conspicuously thickened with a small gap that divides the columella into two distinct folds. Umbilicus absent. Sculpture with a number of irregular spiral lines more conspicuous near the anterior and posterior ends of the shell. Color pale brown.

ANATOMY.—Digestive system containing three smooth and irregular gizzard plates, composed of a thickened central area and a thinner extension (Fig. 4B). Central plate wider than the two lateral plates. Radular formula $16 \times 1.1.1$ in a specimen from Punta Piedra (INB0003540314). Lateral teeth hook-shaped with a wider area below the elongate cusp, bearing 16 long and strong denticles (Fig. 4C). Rachidian teeth broad, with several short denticles decreasing in size towards the laterals of each plate, and a gap with no denticles on the center of each rachidian tooth.

GEOGRAPHIC RANGE.—This species is known from Panama and Costa Rica (Keen 1971).

REMARKS.—*Retusa tabogaensis* was originally described based on several shells collected from Isla Taboga, Panama (Strong and Hertlein 1939). The most distinctive feature of this species was the presence of two denticles on the columella. Examination of the type material and original description revealed that our material from Costa Rica belongs to the same species.

Further anatomical examination of Costa Rican specimens revealed the presence of a radula with lateral teeth bearing an extension under the cusp with several long and strong denticles, and three gizzard plates, composed of a thickened central area and a thinner extension, one of the plates wider than the rest. All these features are consistent with those of *Cylichnella* Gabb, 1873, as defined by Gosliner (1979).

***Cylichnella goslineri* Valdés and Camacho-García, sp. nov.**

(Figs. 4D–F, 5)

TYPE MATERIAL.—*Cylichnella goslineri* sp. nov.: HOLOTYPE: Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 1 specimen, leg. M. Lobo (INB0001497964).

MATERIAL EXAMINED.—Sector Playitas (8°44'19.1980N, 83°21'57.0660W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 15 specimens, leg. M. Lobo (INB0003718957). Four hundred and fifty meters southwest of Playa Blanca (10°03'39.5590N, 84°57'23.0410W), Provincia Puntarenas, 0 m depth, 8 December 1999, 1 shell, leg. M. Calderón (CASIZ 0121109).

Shell morphology.—Length up to 4.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval to elongate, with convex sides (Fig. 4D). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire. Apex rounded, slightly umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly, narrowing gradually at about $\frac{1}{5}$ of its length. Columellar margin slightly thickened, simple, with no folds or denticles. Umbilicus absent. Sculpture with a number of irregular and faint spiral lines. Color uniformly dirty white.

ANATOMY.—Buccal bulb oval to elongate, connecting posteriorly to a short esophagus and the small salivary glands (Fig. 5A). Two strong retractor muscles attach laterally to the buccal bulb. Esophagus opening into a large gizzard, which contains three smooth and irregular gizzard plates, composed of a thickened central area and a thinner extension (Fig. 4E); central plate wider than the

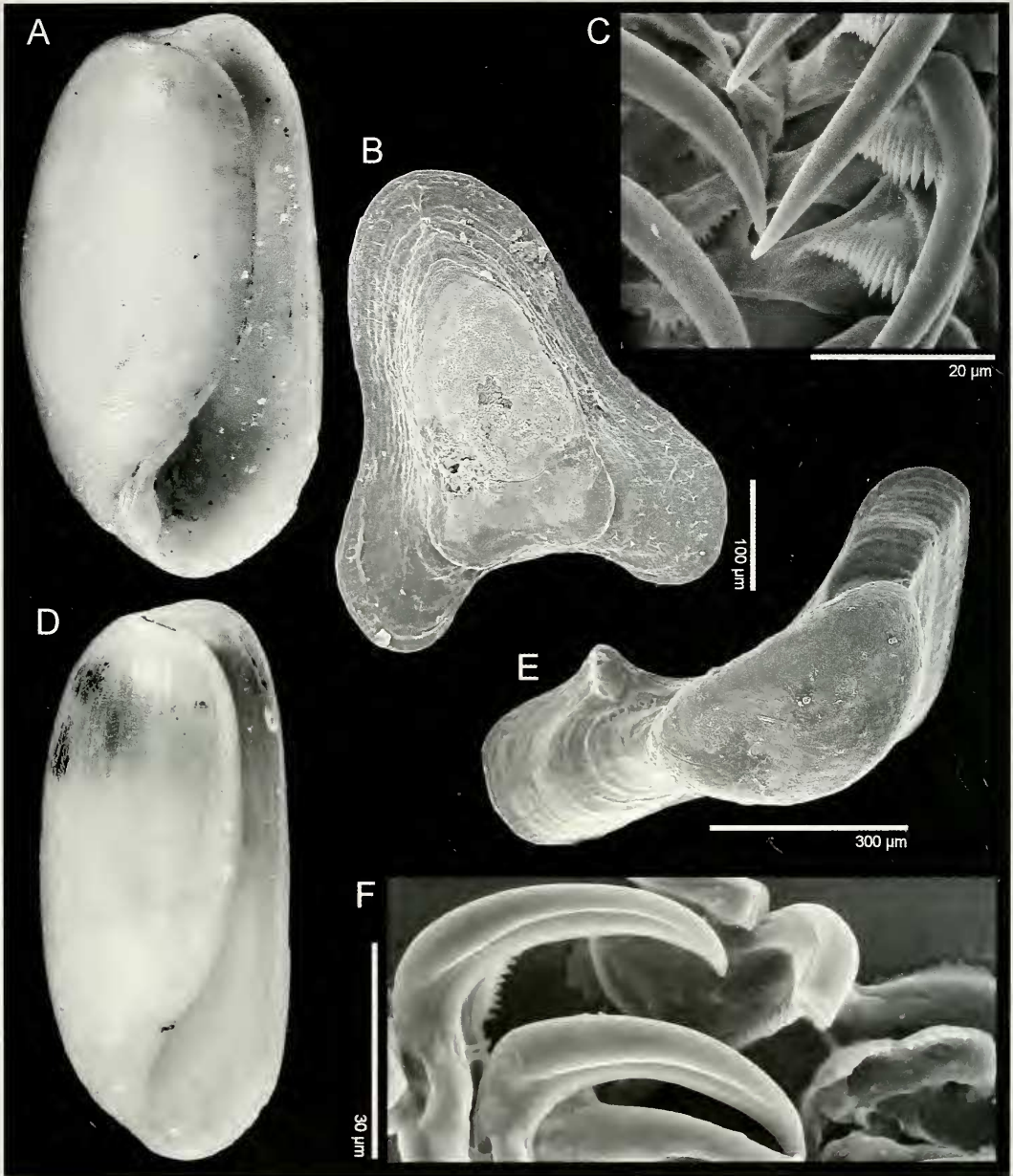


FIGURE 4. A–C, *Cylichnella tabogaensis* (Strong and Hertlein, 1939); (A) Shell morphology, specimen from Bahía Junquillal (INB0003747411), 4 mm long; (B) Central gizzard plate, specimen from Punta Piedra (INB0003540314); (C) Radular teeth, same specimen. D–F, *Cylichnella goslineri* sp. nov.; (D) Shell morphology, Holotype (INB0001497964), 4.5 mm long; (E) Lateral gizzard plate, Paratype from Golfo Dulce (INB0003718957); (F) Radular teeth, same specimen.

two lateral plates. Radular formula $21 \times 1.1.1$ in a specimen from Golfo Dulce (INB0003718957). Lateral teeth hook-shaped, with a wider area below the elongate cusp bearing 12 strong denticles (Fig. 4F). Rachidian teeth broad, with several short denticles decreasing in size towards the laterals of each plate, and a gap with no denticles on the center of each rachidian tooth.

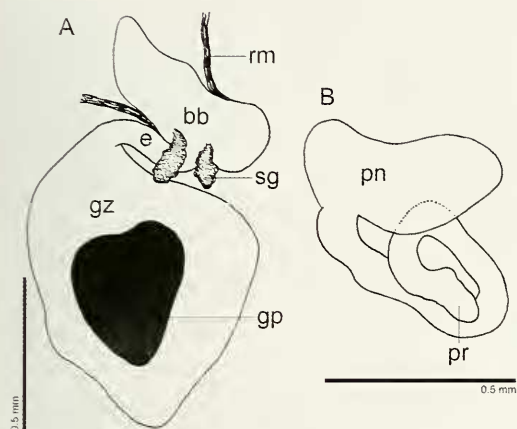


FIGURE 5. *Cylichnella goslineri* sp. nov., anatomy of specimen from Golfo Dulce (INB0003718957); (A) Anterior portion of the digestive system; (B) Male reproductive system. Abbreviations: bb, buccal bulb; e, esophagus; gp, gizzard plate; gz, gizzard; pn, penis; pr, prostate; rm, retractor muscle, sg, salivary gland.

Reproductive system monoaulic. Penis bulbous, connected to the prostate through a long and convoluted duct (Fig. 5B).

GEOGRAPHIC RANGE.—Known from Costa Rica (present paper).

ETYMOLOGY.—The species name is dedicated to our former advisor Terry Gosliner, for his company and support during the field work in Costa Rica.

REMARKS.—*Cylichnella goslineri* sp. nov. is clearly distinct from other *Cylichna*-like opisthobranchs described from the Panamic region by having a more elongate shell with no conspicuous spiral lines. The most similar species in shell morphology is *Cylichna atahualpa*, but these two species clearly differ in the morphology of the radula and gizzard plates (see above). The other member of the genus *Cylichnella* is *C. tabogaensis*, which has a shorter shell with conspicuous spiral lines and radular teeth with stronger denticles.

Cylichnella goslineri sp. nov. is assigned to the genus *Cylichnella* by having a radula with lateral teeth bearing an extension under the cusp with several long and strong denticles, and three gizzard plates, composed of a thickened central area and a thinner extension, one of the plates wider than the rest. All these features are consistent with the definition of this genus by Gosliner (1979).

Family Retusidae Thiele, 1925

Genus *Retusa* Brown, 1827

Retusa paziana Dall, 1919

(Fig. 6A)

Retusa paziana Dall, 1919:297.

TYPE MATERIAL.—*Retusa paziana*: SYNTYPE: La Paz, Mexico (USNM 211418).

MATERIAL EXAMINED.—Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 2 shells (CASIZ 170723). Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 16 shells (CASIZ 170724). Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 1 shell (LACM 33-123.28). Puerto Culebra (10°35'N, 85°40'W), Provincia Guanacaste, 31 m depth, 13 March 1934, 1 shell (LACM 33-153.12). Puerto Culebra (10°37'N, 85°40'W), 27 m depth, 26 February 1933, 1 shell (LACM 34-253.6). Puerto Parker (10°55'N, 85°49'W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.2). Puerto Parker (10°57'50"N, 85°48'45"W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 3 shells (LACM 35-113.25). Bahía Salinas (11°03'33"N, 85°43'47"W), 11 February 1935, 3 shells (LACM 35-117.17). Bahía Salinas (11°03'33"N, 85°44'05"W), 11 February 1935, 2 shells (LACM 35-122.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.47). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.41). Half mile off mouth of Bahía Huevos (10°38'22"N,

85°42'52"W), Provincia Guanacaste, 36–42 m depth, 19 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-36.25). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-40.32). Off beach at Bahía Ballena (9°44'12"N, 84°59'32"W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.39). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 2 shells, leg. J. McLean (LACM 72-54.53). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 1 shell, leg. Y. Camacho (INB0003747060). Isla David (10°56'32.2000N, 85°42'51.1000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 18 m depth, 12 March 1996, 4 shells, leg. Y. Camacho (INB0003700589). Isla David (10°58'45.4310N, 85°43'01.8500W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 0–3 m depth, 13 March 1996, 3 shells, leg. R. Angulo (INB0003747335). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003719254).

SHELL MORPHOLOGY.—Length up to 3 mm; width up to 1 mm in the largest specimen examined. Shell fragile, elongate, wider anteriorly and narrower posteriorly, with nearly parallel or slightly concave sides (Fig. 6A). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire and the apex of the protoconch, which is partially embedded. Apex umbilicated, with the aperture lip rising from the right side. Aperture lip forming a rounded wing connected to the columellar margin. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly and narrowing abruptly at about $\frac{1}{4}$ of its length. Columellar margin slightly thickened. Columella simple, with no folds. Umbilicus absent. Sculpture with a number of conspicuous growth lines crossed by faint spiral lines. Color uniformly whitish.

ANATOMY.—All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.—Known from the Gulf of California (Keen 1971) and Costa Rica.

REMARKS.—Dall (1919) described *Retusa paziana* based on shells from La Paz, Baja California Sur, Mexico, with a short description and no figures. Baker and Hanna (1927) collected additional specimens from the Gulf of California and illustrated this species for the first time. The shells from Costa Rica here examined match the original description and redescription by Baker and Hanna (1927), and there is no doubt they belong to the same species.

Retusa paziana is the only member of *Retusa* from the Panamic region. Its unique shell morphology, with the wider area close to the anterior end, and the sculpture, composed of strong growth lines, make this species easily recognizable.

Retusa sp.

(Fig. 6B)

MATERIAL EXAMINED.—1.5 mile east of Punta Ballena (9°44'15"N, 84°33'45"W), Provincia Guanacaste, 3–15 m depth, 21–22 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-42.61). Playa Nancite (10°48'N, 85°42'W), north side of Golfo Papagayo, Provincia Guanacaste, 15 January 1986, 1 shell, leg. E. Coan and R. Hollywood (LACM 86-26.34).

SHELL MORPHOLOGY.—Length up to 2 mm; width up to 1 mm in the largest specimen examined. Shell fragile, oval, wider near the center, with convex sides (Fig. 6B). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire and the apex of the protoconch, which is partially embedded. Apex umbilicated, with the aperture lip rising from the right side. Aperture lip forming a rounded wing connected to the columellar margin. Anterior end of the shell elongate. Aperture as long as the shell, wider anteriorly and narrowing gradually at about $\frac{1}{4}$ of its length. Columellar margin slightly thickened. Columella simple, with no folds.

Umbilicus very narrow. Sculpture with a number of simple spiral lines crossed by conspicuous growth lines. Color uniformly whitish.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— Known from Costa Rica (present paper).

REMARKS.— This is most likely an undescribed species but it will not be described herein because of the lack of anatomical information. *Retusa* sp. is similar to *Retusa paziana* in some respects but clearly distinguishable by the outline of the shell and sculpture. The shell of *Retusa* sp. has its wider area near the center of the shell, whereas in *R. paziana* it is near the anterior end. Additionally, *Retusa* sp. has a small umbilicus that is absent in *R. paziana*. The sculpture of *R. paziana* is composed of conspicuous growth lines crossed by faint spiral lines whereas in *Retusa* sp. the spiral lines are equally conspicuous.

This species is provisionally placed in the genus *Retusa* because of the morphological similarities of the shell with some other species of the genus.

Genus *Volvulella* Newton, 1891

Volvulella cylindrica (Carpenter, 1864)

(Figs. 6D–E)

Volvula cylindrica Carpenter. 1864:179.

Volvulella callicera Dall. 1919:299.

Volvulella cooperi Dall. 1919:297–298.

Volvulella lowei Strong and Hertlein. 1937:164–165, pl. 35, fig. 2.

TYPE MATERIAL.— *Volvula cylindrica*: HOLOTYPE: Santa Barbara, California (Redpath Museum 2364). *Volvulella callicera*: HOLOTYPE: Galapagos Islands (USNM 194976B). *Volvulella cooperi*: HOLOTYPE: Scammons Lagoon [= Laguna Ojo de Liebre], Baja California Sur, Mexico (USNM 105501). *Volvulella lowei*: HOLOTYPE: Puerto Escondido, Baja California Sur, Mexico (CASIZ 065971).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 38 shells (CASIZ 170718). Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.29). Puerto Culebra (10°35'N, 85°40'W), Provincia Guanacaste, 31 m depth, 13 March 1934, 4 shells (LACM 33-153.13). Puerto Culebra (10°37'N, 85°40'W), Provincia Guanacaste, 27 m depth, 26 February 1934, 1 shell (LACM 34-253.7). Puerto Parker (10°55'N, 85°49'W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.3). Puerto Parker (10°57'50"N, 85°48'45"W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 2 shells (LACM 113.26). Bahía Salinas (11°03'33"N, 85°43'47"W), Provincia Guanacaste, 11 February 1935, 3 shells (LACM 35-117.18). Playa Blanca (10°56'45"N, 85°53'30"W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.7). Playa Blanca (10°56'45"N, 85°53'30"W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.7). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55'15"N, 85°48'30"W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 8 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.16). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-12.47). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02'22"N, 85°45'16"W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.45). Bahía Potrero Grande (10°50'56"N, 85°48'35"W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 6 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.11). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 18 shells,

leg. P. LaFollette and D. Cadien (LACM 72-35.42). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 11 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.33). Anchorage at Bahía Ballena off Tambor (10°44'10"N, 84°59'34"W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 2 shells, leg. P. LaFollette and A. Ferreira (LACM 72-43.18). Off beach at Bahía Ballena (9°44'12"N, 84°59'32"W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.40). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 11 shells, leg. J. McLean (LACM 72-54.54). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.39). Playa Nancite (10°48'N, 85°42'W), north side of Golfo Papagayo, Provincia Guanacaste, 15 January 1986, 2 shells, leg. E. Coan and R. Hollywood (LACM 86-26.35). One km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 1 shell, 5 April 2002, leg. F. González (INB0003503969). One and half km northwest of Playa Junquillal (10°58'40.7139N, 85°42'27.2867W), Bahía Junquillal, Provincia Guanacaste, 20 m depth, 1 shell, 4 April 2002, leg. F. González (INB0003539752). South of Isla Juanilla (10°58'55.1750N, 85°43'10.1707W), Murciélago, Provincia Guanacaste, 15 m depth, 1 shell, 9 April 2002, leg. F. González (INB0003539769). Between Isla Bolaños and Playa Coyotera (11°02'51.0972N, 85°43'21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 2 shells, 10 April 2002, leg. F. González (INB0003539771). Four hundred m west of Isla Cabo Blanco (9°32'29.2960N, 85°07'16.0340W), Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 4 shells, 16 May 1998, leg. A. Berrocal (INB0003539975). Isla David (10°58'05.5000N, 85°42'38.6000), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 19 shells, 12 March 1996, leg. Y. Camacho (INB0003542912). Isla David (10°56'32.2000N, 85°42'51.1000), Santa Rosa, Provincia Guanacaste, 18 m depth, 16 shells, 12 March 1996, leg. Y. Camacho (INB0003575622). Playa Matapalo (9°21'48.1193N, 84°05'33.8006W), National Park Manuel Antonio, Provincia Puntarenas, 10–15 m depth, 1 shell, 18 February 2003, leg. F. González (INB0003708499). Playa Ballena (9°06'34.2870N, 83°41'46.4390W), Uvita, Provincia Puntarenas, 1 m depth, 1 shell, 16 March 1996, leg. Y. Camacho (INB0003722812). Muelle de la Playa San Miguel (9°34'36.9190N, 85°08'06.3610W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 14 shells, 2 May 1995, leg. G. Mena (INB0003722819). Punta Oliva (9°34'39.3370N, 85°08'15.3840W), Cabo Blanco, Provincia Puntarenas, 0 m depth, 12 shells, 16 September 1995, leg. F. Alvarado (INB0003722820). Playa Mostrencal (10°59'47.3060N, 85°42'53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 2 shells, 13 March 1996, leg. R. Angulo (INB0003722825). Bahía Junquillal (10°59'13.0310N, 85°43'16.7950W), Golfo Santa Elena, Provincia Guanacaste, 3 m depth, 5 shells, 13 March 1996, leg. R. Angulo (INB0003722828). Isla David (10°58'45.4310N, 85°43'01.8500W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 0–3 m depth, 9 shells, 13 March 1996, leg. R. Angulo (INB0003747336). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 1 shell, 12 March 1996, leg. R. Angulo (INB0003747062).

SHELL MORPHOLOGY.— Length up to 5.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with nearly parallel sides (Fig. 6D–E). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about $\frac{1}{5}$ of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a conical spine that completely covers the apex. Spine long and more curved in some specimens (Fig. 6D) and shorter and straight in some others (Fig. 6E). Columellar margin thickened, with a small protuberance. Sculpture composed of a number of irregular spiral grooves crossed by numerous fine growth lines all over the shell surface. Spiral grooves situated near the anterior and posterior ends of the shell more conspicuous and separated from each other by wider gaps than those in the center of the shell. Color uniformly shiny whitish.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— Known from southern California to Panama and the Galapagos Islands (Keen 1971).

REMARKS.— Carpenter (1864) described *Volvula cylindrica* from Santa Barbara, California,

based on a single shell. The original description is brief and offers few details. Examination of the holotype, illustrated by Palmer (1958), revealed that the specimens here examined match the original description of this species.

The shell morphology of this species is variable, with some specimens having a more elongate and curved apical spine and other specimens with a short and straight spine. The material examined includes intermediate forms within the entire range of variability.

This shell variability is probably the cause of the introduction of several names for this species. Three synonyms have been recognized in the Panamic Province: *Volvulella callicera* Dall, 1919, from the Galapagos, and *Volvulella cooperi* Dall, 1919 and *Volvulella lowei* Strong and Hertlein, 1937 from the Gulf of California. The study of the type material of all these species confirmed that they all fit within the variability of *V. cylindrica*.

Volvulella californica Dall, 1919, originally described from southern California, was redescribed by Gosliner (1996), who argued that it is a distinct species from *V. cylindrica*. According to Gosliner (1996), *V. californica* is consistently devoid of sculpture and pyriform in shape, whereas *V. cylindrica* has a sculpture and is far more cylindrical.

***Volvulella catharia* Dall, 1919**

(Fig. 6C)

TYPE MATERIAL.— *Volvulella catharia*: SYNTYPE: Bahía de Panama (USNM 211784).

MATERIAL EXAMINED.— Bahía Chatham (5°33'20"N, 86°59'10"W), Cocos Island, 26 m depth, 13 January 1938, 2 shells (LACM 38-179.5). Ten miles off Punta Guiones (9°43.5'N, 85°44.0'W), Provincia Guanacaste, 320–457 m depth, 13 May 1973, 2 shells (LACM 73-65.4).

SHELL MORPHOLOGY.— Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Fig. 6C). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about 1/4 of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a short, blunt protuberance that covers the apex. Columellar margin thickened. Sculpture composed of irregular spiral grooves faded in the specimens examined. Color uniformly pale brown.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— Known from Costa Rica and Panama (Keen 1971).

REMARKS.— Dall (1919) described *Volvulella catharia* as a small species with a short spine at the apex, subcylindrical and smooth. Examination of the holotype (USNM 211784) revealed that the specimens here studied from Costa Rica belong to the same species.

Volvulella catharia is clearly different from other Panamic species of *Volvulella*. The shell of *V. catharia* is shorter and proportionally wider, with a small and rounded apical extension. This species is provisionally placed in *Volvulella* until complete specimens become available for study.

***Volvulella panamica* Dall, 1919**

(Fig. 6F)

Volvulella panamica Dall. 1919:298.

Volvulella tenuissima Willett. 1944:71–72, pl. 14, fig. 1.

TYPE MATERIAL.— *Volvulella panamica*: HOLOTYPE: Bahía de Panama (USNM 212654). *Volvulella tenuissima*: HOLOTYPE: LACM 1073 (1 dry shell) 137 m, off Redondo Beach, Los Angeles County, California.

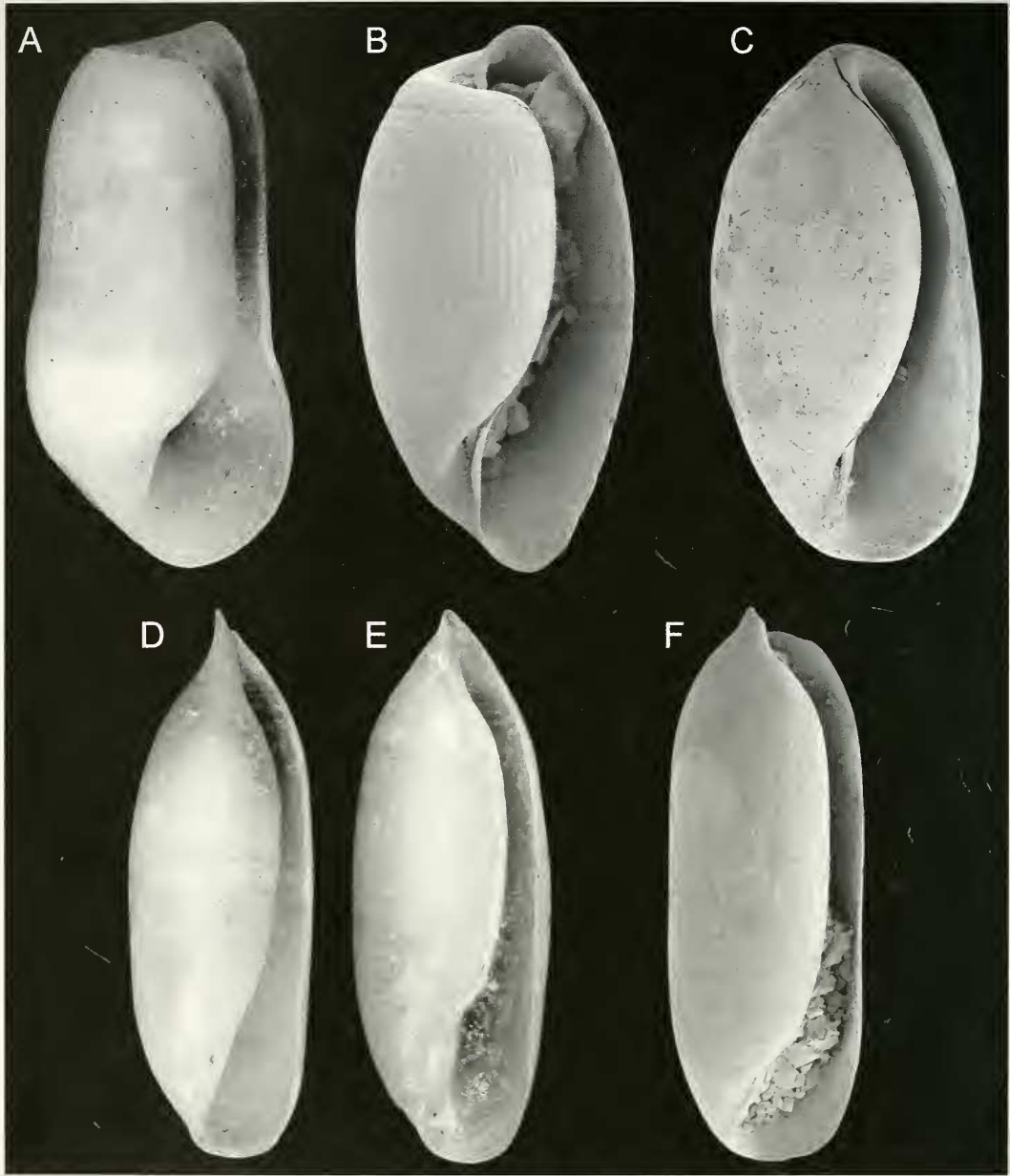


FIGURE 6. A. *Retusa paziana* Dall, 1919, shell morphology, specimen from Isla David (INB0003719254), 2.5 mm long. B. *Retusa* sp., shell morphology, specimen from Punta Ballena (LACM 72-42.61), 1.8 mm long. C. *Volvulella catharia* Dall, 1919, shell morphology, specimen from Punta Guiones (LACM 73-65.4), 4 mm long. D–E, *Volvulella cylindrica* (Carpenter, 1864): (D) Shell morphology, specimen from Bahía Junquillal. (INB0003747336), 5 mm long; (E) Shell morphology, specimen from Bahía Brasilito, 4 mm long (LACM 72-40.33). F. *Volvulella panamica* Dall, 1919, shell morphology, specimen from Bahía Herradura (LACM 72-54.55), 5.5 mm long.

MATERIAL EXAMINED.— Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra. Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.30). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 7 shells, leg. J. McLean (LACM 72-54.55).

SHELL MORPHOLOGY.— Length up to 5.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with nearly parallel sides (Fig. 6F). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about 1/5 of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a short spine that completely covers the apex. Spine sharp and narrow because of the presence of a rounded notch on the posterior end of the spire. Columellar margin thickened, with a small protuberance. Sculpture composed of a number of irregular spiral grooves crossed by numerous fine growth lines all over the shell surface. Spiral grooves situated near the anterior and posterior ends of the shell more conspicuous and separated from each other by wider gaps than those in the center of the shell. Color uniformly shiny whitish.

ANATOMY.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

GEOGRAPHIC RANGE.— This species is known from southern California to Panama (Keen 1971; Gosliner 1996).

REMARKS.— *Volvulella panamica* was described by Dall (1919) on the basis of a single shell from Panama Bay that had a very short and sharp apical spine. Examination of the holotype (USNM 212654) revealed that the spine morphology is caused by the presence of a rounded notch on the posterior end of the spire, not by shell damage or a preservation artifact. Examination of several shells from Costa Rica of different sizes revealed a similar morphology of the apex, which sustains the separation of this species from *Volvulella cylindrica*.

Volvulella tenuissima, originally described from southern California by Willett (1944) has a similar morphology and constitutes a synonym. The study of the holotype (LACM 1073), showed the presence of the sharp apical spine typical of this species.

Family Haminoeidae Pilsbry, 1895

Genus *Haminoea* Turton, 1830

Haminoea ovalis Pease, 1868

(Figs. 7A, 8A–C, 9)

Haminoea ovalis Pease, 1868:71, pl. 7, fig. 2, pl. 12, fig. 20.

TYPE MATERIAL.— *Haminoea ovalis*: Untraceable.

MATERIAL EXAMINED.— Punta Uvita (9°08'44.4560N, 83°45'42.2750W), Provincia Puntarenas, 0 m depth, 1 shell, 13 April 1996, leg. R. Angulo (INB0001486877). 500 m south of Playa Ventanas (9°05'16.1660N, 83°40'50.7600W), Provincia Puntarenas, 0 m depth, 2 specimens, 17 January 2000, leg. M. Calderón (INB0001495966). 500 m south of Playa Ventanas (9°05'16.1660N, 83°40'50.7600W), Provincia Puntarenas, 0 m depth, 1 specimen, 17 January 2000, leg. M. Calderón (INB0001496120). San Miguel (9°34'49.0680N, 85°08'28.5260), Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001496693). San Miguel (9°34'49.0680N, 85°08'28.5260), Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001496694). Puerto Escondido (9°23'02.7920N, 84°08'14.4875W), National Park Manuel Antonio, Provincia Puntarenas, 0 m depth, 3 specimens, 19 February 2003, leg. A. Berrocal (INB0003572107). National Park Manuel Antonio (9°23'02.6451N, 84°10'05.9237W), Provincia Puntarenas, 8–11 m depth, 1 specimen, 19 February 2003, leg. A. Berrocal (INB0003572120). Isla Ballena (9°06'18.0003N, 83°43'42.7017W), Provincia Puntarenas, 18 m depth, 18 January 2003, 1 specimen, leg. S. Ávila (INB0003572558). Isla Santa Catalina (10°28'37.2000N,

85°52'06.6000W), Provincia Guana-
caste, 15 m depth, 21 July 2000, 2
specimens, leg. M. Calderón
(INB0003701269).

SHELL MORPHOLOGY.—

Length up to 4 mm; width up to 3
mm in the largest specimen
examined. Shell fragile, delicate,
oval, with convex sides (Fig.
8A). Only one whorl visible,
forming the entire shell. Apex
rounded, with the aperture lip ris-
ing from the left side. Anterior
end of the shell rounded.
Umbilicus absent. Aperture long,
wide anteriorly, narrowing grad-
ually at about $\frac{1}{2}$ of its length.
Columellar margin slightly thick-
ened. Surface smooth, the sculp-
ture being reduced to fine growth
lines. Color uniformly pale
brown.

EXTERNAL MORPHOLOGY.—

Body oval, 6 mm long in the
largest specimen examined.
Cephalic shield elongate, nar-
rower posteriorly, comprising
about $\frac{1}{2}$ of the body length (Fig.
7A). Hancock's organs com-
posed of about 6 simple folds
each. Parapodia short and nar-
row, covering a small portion of
the shell laterally. Posterior half
of the body almost entirely cov-
ered by the shell. Gill unipinnate,
with 15 simple lamellae. Color of
living animals pale bluish gray,
with darker areas on anterior cen-
tral region of the cephalic shield
and the posterior lateral sides, as
well as in some irregular areas on
the rest of the body. Entire sur-
face of the body covered by
small and bright orange dots. Shell translucent, almost transparent. Area covered by the shell clearly visible, with the same color as the rest of the body and the orange dots larger in diameter.

ANATOMY.—Buccal bulb oval to elongate, connecting posteriorly to a short esophagus and two long salivary glands (Fig. 9A). Esophagus opening into a large gizzard, which contains three

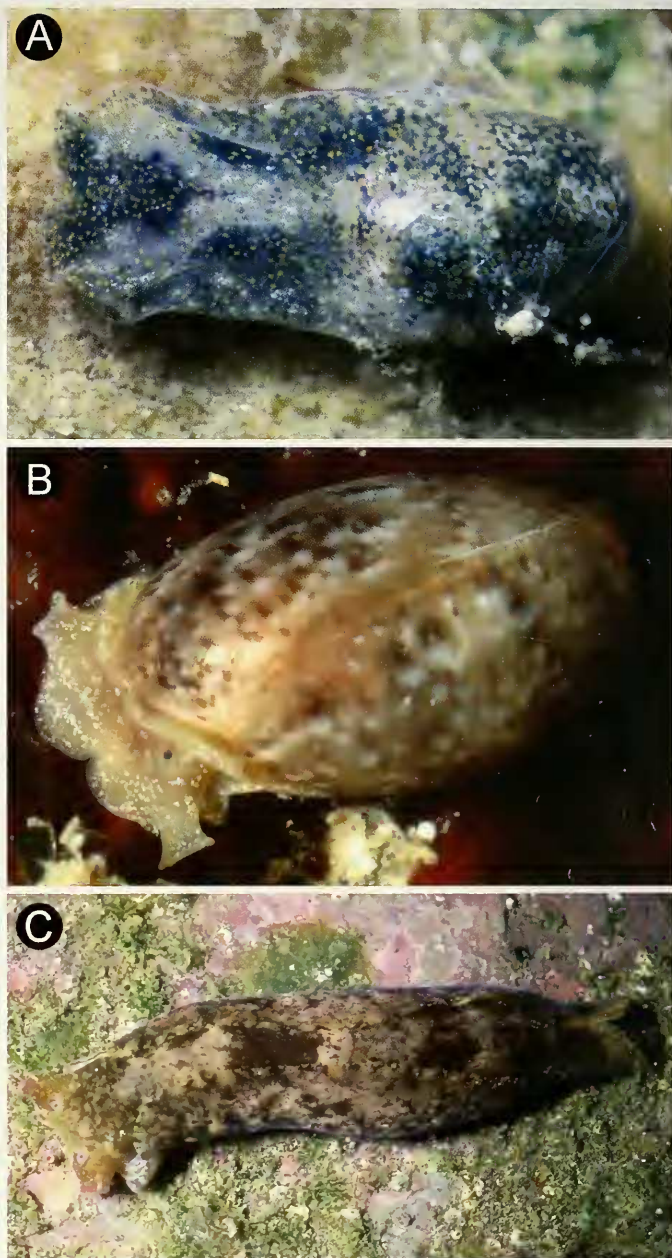


FIGURE 7. Living animals; (A) *Haminoea ovalis* Pease, 1868; (B) *Bulla punctulata* A. Adams in Sowerby, 1850; (C) *Navanax aenigmaticus* (Bergh, 1894).

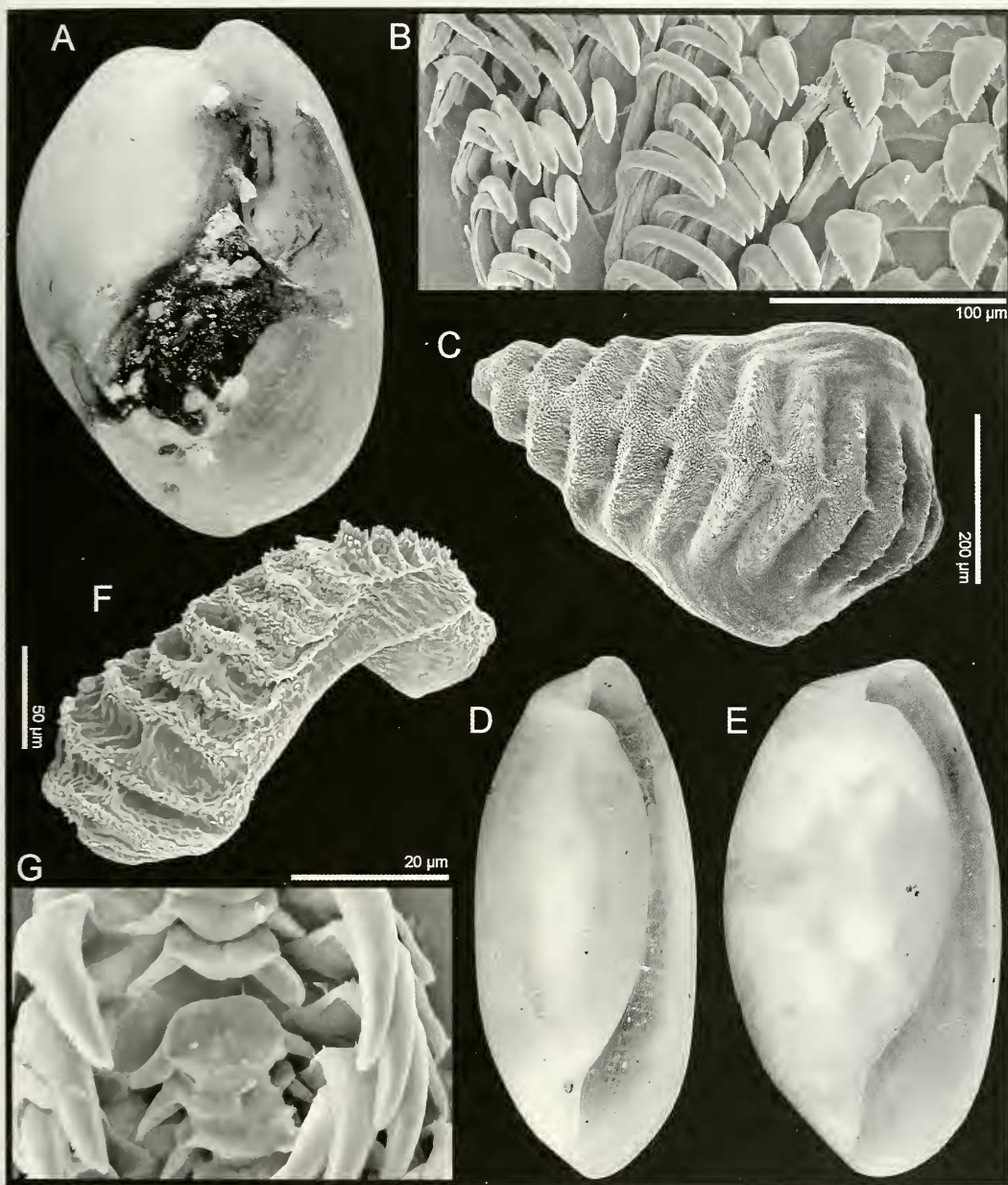


FIGURE 8. A–C, *Haminoea ovalis* Pease, 1868; (A) Shell morphology, specimen from Punta Uvita (INB0001486877), 4 mm long; (B) Radular teeth, specimen from Isla Ballena (INB0003572558); (C) Gizzard plate, same specimen. D–G, *Atys exarata* Carpenter, 1857; (D) Shell morphology, specimen from Punta Descartes (INB0003747331), 5 mm long; (E) Shell morphology, specimen from between Punta Piedra and Punta Gallardo (INB0003540313), 4 mm long; (F) Gizzard plate, specimen from Punta Piedra (INB0001496350); (G) Radular teeth, same specimen.

smooth and irregular gizzard plates. All plates are similar in shape and size, each one having a series of transverse, parallel ridges composed of several rows of small, simple denticles (Fig. 8C).

Radular formula $19 \times 11.1.11$ in a specimen from Isla Ballena (INB0003572558). First inner-

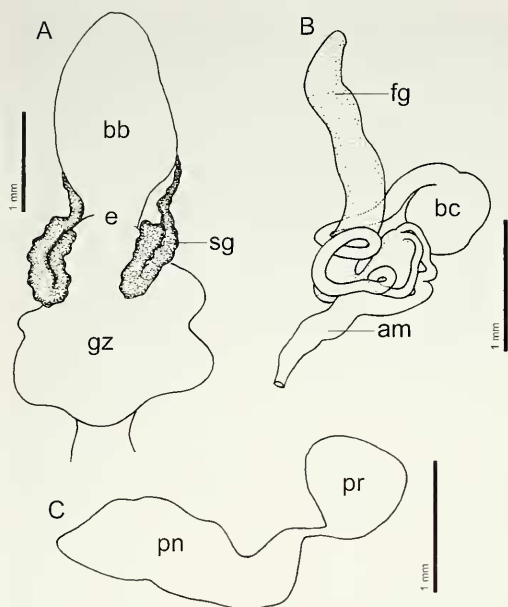


FIGURE 9. *Haminoea ovalis* Pease, 1868, anatomy of specimen from Isla Ballena (INB0003572558); (A) Anterior portion of the digestive system; (B) Female reproductive system; (C) Male reproductive system. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; e, esophagus; fg, female glands; gz, gizzard; pn, penis; pr, prostate; sg, salivary gland.

most teeth with a wide triangular cusp bearing several small denticles (Fig. 8B). Lateral teeth hook-shaped with a strong cusp lacking denticles. Rachidian teeth broad, with a wide base, a single central cusp, and one denticle on each side of the cusp.

Reproductive system monoaulic. Penis bulbous, connected to the prostate through a short duct (Fig. 9C). Ampulla long and convoluted, connecting to a short and wide post-ampullary duct that opens into the female glands. Bursa copulatrix entering the female glands (Fig. 9B).

GEOGRAPHIC RANGE.— This is a widespread Indo-Pacific species. This is the first record of the species for the eastern Pacific.

REMARKS.— The specimens here examined resemble the external coloration of *Haminoea ovalis* Pease, 1868, originally described from Tahiti, French Polynesia. *Haminoea angelensis* Baker and Hanna, 1927, was described on the basis of shell morphology (Baker and Hanna 1927), so it is impossible to determine its taxonomic status. Two other Panamic species, *Haminoea vesicula* (Gould, 1855) and *Haminoea virescens* (Sowerby, 1833) have been illustrated by Behrens (1991) and clearly differ from *H. ovalis* by lacking the bright orange spots characteristic of this species.

Genus *Alys* de Monfort, 1810

Alys exarata (Carpenter, 1857)

(Figs. 8D–G)

Bulla exarata Carpenter, 1857:173.

Alys casta Carpenter, 1864:314.

Alys chimera Baker and Hanna, 1927:126, pl. 4, fig. 4.

Cylichna veleronis Strong and Hertlein, 1939:191.

Cylichna stephensae Strong and Hertlein, 1939:190.

Alys liriopae Hertlein and Strong, 1951:71, pl. 8, fig. 2.

TYPE MATERIAL.— *Bulla exarata*: HOLOTYPE: Mazatlán, Sinaloa, Mexico (BMNH). *Alys casta*: LECTOTYPE and PARALECTOTYPE: Cabo San Lucas, Baja California Sur, Mexico (USNM 4014). *Alys chimera*: HOLOTYPE: Puerto Escondido, Baja California Sur, Mexico (CASIZ 032115). *Cylichna veleronis*: PARATYPE: Bahía Honda, Isla Coiba, Panama (LACM 1340). *Cylichna stephensae*: PARATYPE: Bahía Honda, Isla Coiba, Panama (LACM 1339). *Alys liriopae*: HOLOTYPE: Arena Bank, Gulf of California (CASIZ 065495).

MATERIAL EXAMINED.— Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 5 shells (LACM 33-123.31). Playa Blanca (10°56'45"N,

85°53'30"W). Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.9). Playa Blanca (10°56'45"N, 85°53'30"W), Bahía Playa Blanca, Provincia Guanacaste, 73 m depth, 1935, 8 shells (LACM 35-103.15). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55'15"N, 85°48'30"W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.17). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02'22"N, 85°45'16"W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 13 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.46). Cove between Isla San José and Isla Cocinero (10°51'50"N, 86°55'30"W), Islas Murciélago, Provincia Guanacaste, 3–11 m depth, 17 February 1972, 1 shell, leg. P. LaFollette, D. Cadien and A. Ferreira (LACM 72-21.19). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 17 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.43). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 16 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.34). Off beach at Bahía Ballena (9°44'12"N, 84°59'32"W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 7 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.41). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.40). North side of Isla del Caño (8°43'15"N, 83°53'07"W), Provincia Puntarenas, 7–14 m depth, 14–19 March 1972, 6 shells, leg. J. McLean and D. Wheeler (LACM 72-63.80). 250 m off Punta Piedra (8°35'24.6720N, 83°11'26.3250W), Provincia Puntarenas, 23 m depth, 14 April 1997, 12 shells, leg. M. Lobo (INB0001496350). 1 km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590), Provincia Guanacaste, 30 m depth, 5 April 2002, 1 shell, leg. F. González (INB0003503527). 1 km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590), Provincia Guanacaste, 30 m depth, 5 April 2002, 1 shell, leg. F. González (INB0003503528). South of Isla Juanilla (10°58'55.1750N, 85°43'10.1707W), Murciélago, Provincia Guanacaste, 15 m depth, 2 shells, 9 April 2002, leg. F. González (INB0003504414). From 500 m off the beach to 2.5 km southeast (8°34'39.1040N, 83°11'29.6540W), Punta Piedra, Provincia Puntarenas, 14–90 m depth, 10 April 1997, 25 shells, leg. M. Madrigal (INB0003540313). Between Punta Piedra and Punta Gallardo (8°35'47.5010N, 83°11'58.9990W), Provincia Puntarenas, 30–35 m depth, 13 June 1997, 8 shells, leg. M. Madrigal (INB0003540366). 1 km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 4 shells, 5 April 2002, leg. F. González (INB0003542436). Isla David (10°56'32.2000N, 85°42'51.1000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 2 shells, leg. Y. Camacho (INB0003575625). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 2 shells, leg. S. Ávila (INB0003575665). Playa Blanca (8°38'18.0525N, 83°26'15.7570W), Provincia Puntarenas, 0 m depth, 5 April 1995, 1 shell, leg. G. Mena (INB0003722817). Bahía Junquillal (10°58'45.4310N, 85°43'01.8500W), Provincia Guanacaste, 0–3 m depth, 1 shell, 13 March 1996, leg. R. Angulo (INB0003722829). Boca de Estero Caballero (8°40'06.3050N, 83°26'41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0003747046). Golfo Santa Elena (10°59'13.0310N, 85°43'16.7950W), Bahía Junquillal, Provincia Guanacaste, 3 m depth, 13 March, 1996, 1 shell, leg. R. Angulo (INB0003747330). Punta Descartes (11°02'21.8310N, 85°43'11.0470W), Playa Coyotera, Provincia Guanacaste, 0 m depth, 14 March 1995, 1 shell, leg. G. Bassey (INB0003747331).

SHELL MORPHOLOGY.—Length up to 6 mm; width up to 3 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Figs. 8D–E). Shell morphology very variable, some specimens are wider (Fig. 8E) whereas others are more elongate (Fig. 8D). Only one whorl visible, forming the entire shell. Apex rounded, depressed, not umbilicated, with the aperture lip conspicuously rising from the left side. The aperture lip forms a short wing posteriorly, longer in some specimens (Fig. 8D). Anterior end of the shell rounded. Umbilicus absent. Aperture long, wide anteriorly, narrowing at about $\frac{1}{3}$ of its length continuing in a narrow canal to the end of the shell where it widens again. Columellar margin slightly oblique, with a thickened margin and no folds. Sculpture with a number of simple spiral grooves, less conspicuous in the middle area of the shell, and more densely concentrated near the anterior and posterior ends. Color uniformly whitish to pale gray.

ANATOMY.—Digestive system with a gizzard containing three irregular gizzard plates. Each

plate has a series of transverse, parallel ridges composed of small, simple denticles (Fig. 8F). All plates are similar in shape and size. The radular formula is $23 \times 5.1.5$ in a specimen from Punta Piedra (INB0001496350). The innermost lateral teeth are hook-shaped with a long and strong cusp bearing numerous denticles (Fig. 8G). The remaining four lateral teeth have a simple cusp, with no denticles. The rachidian teeth are broad, with a triangular base and a wide central cusp lacking denticles.

GEOGRAPHIC RANGE.— Known from southern California to Panama (Skoglund 2002).

REMARKS.— *Bulla exarata* was introduced based on a shell collected from Mazatlán, Sinaloa, Mexico, with a short description with no illustrations. The holotype of this species (BMNH) is an elongate shell with numerous and conspicuous longitudinal striations and the aperture lip conspicuously rising from the left side. These and other features of the specimen are very similar to those of the material here examined.

A few years later, Carpenter (1864) described *Atys casta*, with a short text and no illustrations, based on a single shell collected from Cabo San Lucas, Baja California Sur, Mexico. Baker and Hanna (1927) considered the description of *A. casta* “so vague and indefinite that identifications based thereupon would be entirely untrustworthy.” Consequently these authors introduced a new name, *Atys chimera* for similar shells collected from Puerto Escondido, La Paz, and Bahía Concepción, Baja California Sur, Mexico. A re-examination of a syntype of *Atys casta* (USNM 4014) revealed that this specimen is very similar in shell morphology to the specimens here examined, which also agrees with the original description of *A. chimera* and the features of the holotype (CASIZ 032115).

Three other synonyms of *Atys exarata* are *Cylichna veleronis* Strong and Hertlein, 1939, *Cylichna stephensae* Strong and Hertlein, 1939, and *Atys liriopae* Hertlein and Strong, 1951. Both *C. veleronis* and *C. stephensae* were described based on shells dredged from Bahía Honda, Panama, and were only compared to species of *Cylichna*. Examination of the type material of these two taxa shows remarkable similarities with the material here examined and all the shells fit within the variability described for this species. *Cylichna stephensae* was described for wider shells with fewer and more distant spiral lines, whereas *C. veleronis* was described for narrower shells with more highly compressed spiral lines.

Atys liriopae was described by Hertlein and Strong (1951) as different from *Atys chimera* by having a more closely spaced and conspicuous sculpture. These differences are explainable by the normal variability of the species, and there is no doubt that *A. liriopae* is a synonym of *A. exarata*.

This species is placed in *Atys* because of the presence of transverse, parallel ridges composed of denticles in the gizzard plates, and the radular morphology, which has broad rachidian teeth, with a wide triangular base and a broad central cusp bearing numerous small denticles as well as hook-shaped lateral teeth with a long and strong cusp bearing numerous denticles on the inner lateral teeth.

Atys defuncta (Baker and Hanna, 1927)

(Figs. 10A–D)

Cylichmella defuncta Baker and Hanna, 1927:127–128, pl. 4, fig. 3.

TYPE MATERIAL.— *Cylichmella defuncta*: HOLOTYPE: Bahía Amortajada, Isla San José, Baja California Sur, Mexico (CASIZ 032118).

MATERIAL EXAMINED.— Bahía Cocos (10°33'35"N, 85°42'30"W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.33). Puerto Culebra (10°35'N, 85°40'W), Provincia Guanacaste, 31 m depth, 13 March 1934, 8 shells (LACM 33-153.14). Bahía Chatham (5°33'N,

86°59'W), Cocos Island, 31 m depth, 28 February 1933, 7 shells (LACM 33-154.1). Puerto Parker (10°55'N, 85°49'W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.4). Bahía Chatham (5°33'20"N, 86°59'10"W), Cocos Island, 26 m depth, 13 January 1938, 1 shell (LACM 38-179.6). Playa Blanca (10°56'45"N, 85°53'30"W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 29 shells (LACM 35.100.10). Puerto Parker (10°57'50"N, 85°48'45"W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 9 shells (LACM 35-113.28). Bahía Salinas (11°03'33"N, 85°44'05"W), Provincia Guanacaste, 11 February 1935, 9 shells (LACM 35-122.17). Between Punta Isla and 500 m south of Punta Isla (10°56'00"N, 85°48'55"W), Bahía Santa Elena, Provincia Guanacaste, 1–11 m depth, 13 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-7.34). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57'20"N, 85°46'08"W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.49). Southeast corner of Bahía Jobo, off sand beach west of Bahía de Salinas (11°02'22"N, 85°45'16"W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 24 shells, leg. P. LaFollette and D. Cadien (LACM 72-21.47). Cove between Isla San José and Isla Cocinero (10°51'50"N, 86°55'30"W), Islas Murciélago, Provincia Guanacaste, 3–11 m depth, 17 February 1972, 1 shell, leg. P. LaFollette, D. Cadien, and A. Ferreira (LACM 72-21.20). Bahía Potrero Grande (10°50'56"N, 85°48'35"W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 5 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.13). South tip of Punta Santa Elena (10°53'35"N, 85°57'52"W), Provincia Guanacaste, 12–15 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-30.27). 5 miles north west of Islas Huevos (10°41'45"N, 85°46'25"W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34.30). Middle of Bahía Huevos, north of Bahía Culebra (10°38'41"N, 85°41'55"W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 11 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.45). Off beach at Bahía Brasilito (10°25'57"N, 85°49'18"W), Provincia Guanacaste, 18 m depth, 20 February 1972, 46 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.36). 1.5 mile east of Punta Ballena (9°44'15"N, 84°33'45"W), Provincia Guanacaste, 3–15 m depth, 21–22 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-42.62). Anchorage at Bahía Ballena off Tambor (10°44'10"N, 84°59'34"W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 30 shells, leg. P. LaFollette and A. Ferreira (LACM 72-43.19). Off beach at Bahía Ballena (9°44'12"N, 84°59'32"W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.42). Bahía Herradura (9°38'45"N, 84°40'55"W), Provincia Puntarenas, 9–17 m depth, 9–10 March 1972, 4 shells, leg. J. McLean (LACM 72-52.63). Bahía Herradura (9°37'58"N, 84°40'30"W), Provincia Puntarenas, 21 m depth, 9 March 1972, 31 shells, leg. J. McLean (LACM 72-53.30). Off Bahía Herradura (9°38'50"N, 84°40'50"W), Provincia Puntarenas, 37 m depth, 10 March 1972, 30 shells, leg. J. McLean (LACM 72-54.57). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 21 m depth, 11 March 1972, 29 shells, leg. J. McLean (LACM 72-57.41). Small islets off Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 9–23 m depth, 11–13 March 1972, 3 shells, leg. J. McLean (LACM 72-58.59). Small islets off Punta Quepos (9°22'12"N, 84°09'15"W), Provincia Puntarenas, 23 m depth, 12 March 1972, 2 shells, leg. J. McLean (LACM 72-59.31). North side of Isla del Caño (8°43'15"N, 83°53'07"W), Provincia Puntarenas, 7–14 m depth, 14–19 March 1972, 26 shells, leg. J. McLean and D. Wheeler (LACM 72-63.81). Isla del Caño (8°44'00"N, 83°52'30"W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 27 shells, leg. J. McLean (LACM 72-64.19). 1.5 km northwest of Playa Junquillal (10°58'40.7139N, 85°42'27.2867W), Provincia Guanacaste, 20 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003501383). Manuel Antonio National Park (9°22'36.6614N, 84°09'23.2807W), Provincia Puntarenas, 15–20 m depth, 1 specimen, 17 February 2003, leg. F. González (INB0003575268). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 4 shells, 12 March 1996, leg. R. Angulo (INB0003575678). Isla David (10°56'06.0000N, 85°42'53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 6 shells, 12 March 1996, leg. R. Angulo (INB0003575681). National Park Manuel Antonio (9°22'36.6614N, 84°09'23.2807W), Provincia Puntarenas, 15–20 m depth, 4 shells, 17 February 2003, leg. F. González (INB0003707722). La Viuda Rock (8°36'56.0065N, 83°14'08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722832). Boca de Estero Caballero (8°40'06.3050N, 83°26'41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0003747045). Playa Mostrencal

(10°59'47.3060N, 85°42'53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 1 shell, 13 March 1996, leg. R. Angulo (INB0003747048). Playa Mostrencal (10°59'47.3060N, 85°42'53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March 1996, leg. R. Angulo (INB0003747334). Playa Mostrencal (10°59'47.3060N, 85°42'53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March 1996, leg. R. Angulo (INB0003747410). Isla David (10°58'05.5000N, 85°42'38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003747596).

SHELL MORPHOLOGY.—Length up to 5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with convex sides, much wider in the central area (Fig. 10A–B). Only one whorl visible, except for a visible portion of the top of the spire. Apex umbilicated with the aperture lip conspicuously rising from the left side, forming a rounded wing connected to the columellar margin. Anterior end of the shell elongate. Umbilicus wide and deep. Aperture long, wider anteriorly, narrowing at about $\frac{1}{3}$ of its length and widening again near the apex. Columella with a single, conspicuous fold. Sculpture with several spiral grooves near the anterior and posterior ends of the shell, absent from the middle area. Color uniformly dirty white.

ANATOMY.—Digestive system with a gizzard containing three irregular gizzard plates. Each plate with a series of transverse, parallel ridges composed of small, simple denticles (Fig. 10C). All plates similar in shape and size. Radular formula $10 \times 3.1.3$ in a specimen from Manuel Antonio (INB0003575268). Lateral teeth hook-shaped with a long and strong cusp bearing numerous denticles (Fig. 10D). Rachidian teeth broad, with a wide triangular base and a broad central cusp bearing numerous small denticles.

REMARKS.—The shell morphology of the specimens here examined is identical to the original description of *Cylichnella defuncta* by Baker and Hanna (1927). This species was originally described in the genus *Cylichnella* and subsequently transferred to *Acteocina* by Skoglund (2002), based on the synonymization of *Cylichnella* with *Acteocina* by Mikkelsen and Mikkelsen (1984).

However, the anatomy of *Cylichnella defuncta* is very different from those of *Acteocina* and *Cylichnella*. The gizzard plates have a series of transverse, parallel ridges composed of small, simple denticles, and the radula has broad rachidian teeth, with a wide triangular base and a broad central cusp bearing numerous small denticles as well as hook-shaped lateral teeth with a long and strong cusp bearing numerous denticles. All these anatomical features as well as the shell morphology, characterized by the presence of striae near the posterior and anterior ends of the shell and the outer lip clearly rising over the apex, are typical of the genus *Atys*. Therefore *C. defuncta* is here regarded as a member of *Atys*.

Family Bullidae Gray, 1827

Genus *Bulla* Linnaeus, 1758

Bulla punctulata A. Adams in Sowerby, 1850

(Figs. 7B, 10E–G, 11)

Bulla punctata A. Adams in Sowerby, 1848–50 [1850]:577, pl. 123, fig. 77 (non *Bulla punctata* Schroeter, 1804).

Bulla punctulata A. Adams in Sowerby, 1848–50 [1850]:604.

TYPE MATERIAL.—*Bulla punctata*: SYNTYPES (2): Panama (BMNH 19760047).

MATERIAL EXAMINED.—Playa Ocotal, Provincia Guanacaste, 14 May 1976, 8 shells, leg. A. Hardy and R. Hardy (CASIZ 048833). Puerto Culebra, Provincia Guanacaste, 1 shell (CASIZ 017943). Cove on northwest side of Isla San Pedrito (10°51'30"N, 86°57'57"W), Islas Murciélago, Provincia Guanacaste, 2–4 m depth, 17 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-22.13). Islas Tortugas,

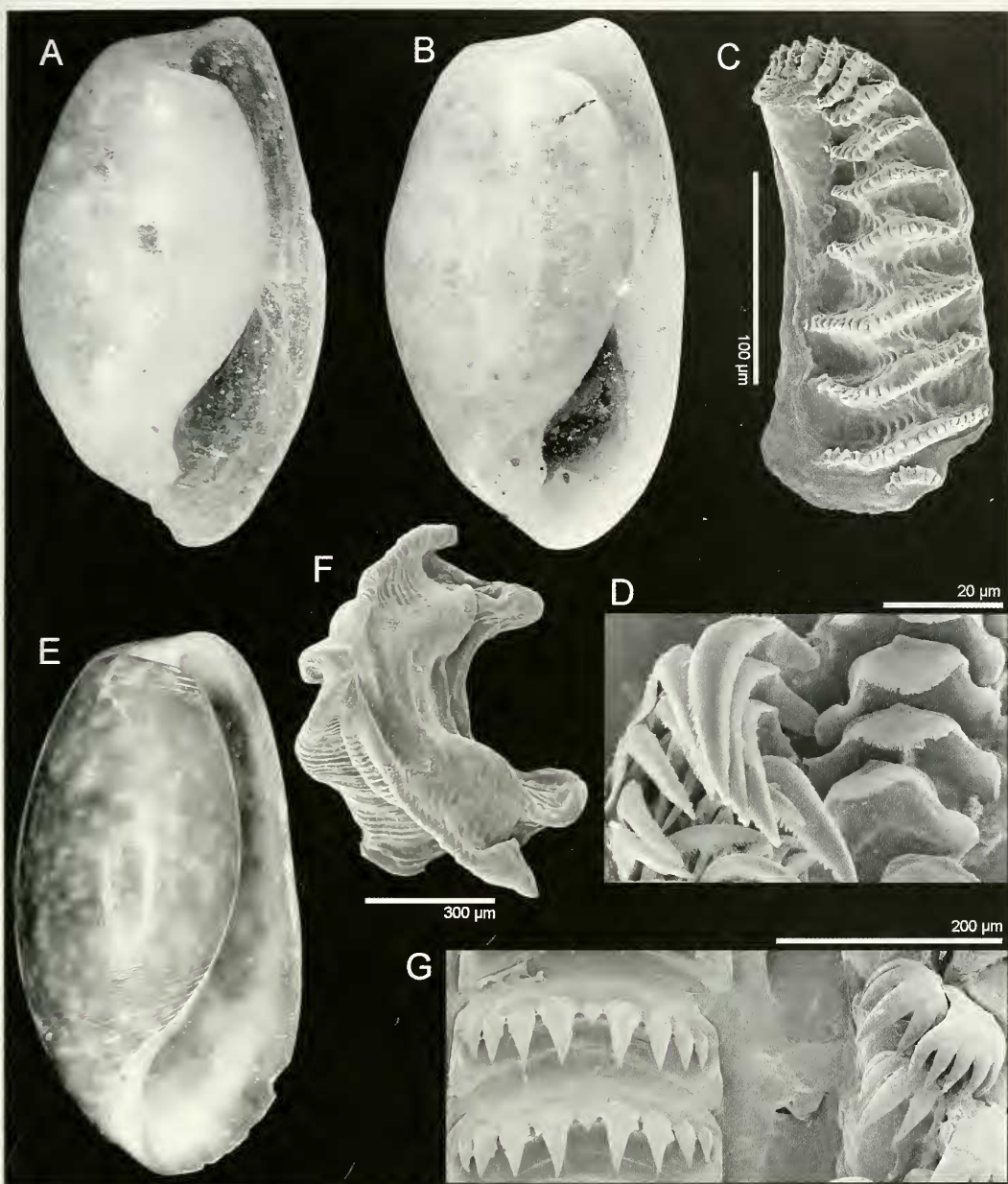


FIGURE 10. A–D. *Atys defuncta* (Baker and Hanna, 1927); (A) Shell morphology, specimen from Playa Junquillal (INB0003501383); 3 mm long; (B) Shell morphology, specimen from Parque Nacional Manuel Antonio, (INB0003575268) 3 mm long; (C) Gizzard plate, same specimen; (D) Radular teeth, same specimen. E–G, *Bulla punctulata* A. Adams in Sowerby, 1850; (E) Shell morphology, specimen from Golfo Dulce (INB0003540757), 7.5 mm long; (F) Gizzard plate, specimen from Isla Bolaños and Playa Coyotera (INB0003502783); (G) Radular teeth, same specimen.

Provincia Puntarenas, 2–8 m depth, 23–24 February 1972, 7 shells, leg. P. LaFollete, D. Cadien, and A. Ferreira (LACM 72-46.59). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22'43"N, 84°09'41"W), Provincia Puntarenas, 21 m depth, 11 March 1972, 4 juvenile shells, leg. J. McLean (LACM 72-57.42). Isla del Caño (8°44'00"N, 83°52'30"W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 1 juvenile shell, leg. J. McLean (LACM 72-64.20). Boca del Estero Caballero (8°40'06.3050N, 83°26'41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0001499756). Murciélago (10°58'14.7752N, 85°42'04.1162W), Provincia Guanacaste, 20 m depth, 5 specimens, 6 April 2002, leg. F. González (INB0003461244). 200 m northwest of Playa Guaría (10°57'55.1620N, 85°42'23.7922W), Bahía Junquillal, Provincia Guanacaste, 8 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003500963). Bahía Tomás (10°55'44.7444N, 85°43'15.9105W), Murciélago, Provincia Guanacaste, 1 m depth, 3 juvenile shells, 9 April 2002, leg. F. González (INB0003501262). Bahía Tomás (10°55'44.7444N, 85°43'15.9105W), Murciélago, Provincia Guanacaste, 1 m depth, 2 shells, 9 April 2002, leg. F. González (INB0003501266). Between Isla Bolaños and Playa Coyotera (11°02'51.0971N, 85°43'21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 10 April 2002, 2 specimens, leg. F. González (INB0003502783). 1 km west of Playa Junquillal (10°58'24.5393N, 85°42'04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 5 April 2002, 5 shells, leg. F. González (INB0003504311). Between Playa Palma and Playa Bejuco (8°43'10.6630N, 83°25'19.9570W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 8 November 1996, 1 shell, leg. M. Lobo (INB0003540757). Bahía Santa Elena (10°54'48.0420N, 85°48'18.5810W), Provincia Guanacaste, 0 m depth, 4 shells, 16 February 1994, leg. G. Bassey (INB0003542096). Isla Ballena (9°06'18.0003N, 83°43'42.7017W), Provincia Puntarenas, 18 m depth, 18 January 2003, 1 specimen, leg. S. Ávila (INB0003572555).

SHELL MORPHOLOGY.—Length up to 7 mm; width up to 5 mm in the largest specimen examined. Shell solid, oval, with convex sides (Fig. 10E). Only one whorl visible, forming the entire shell. Apex rounded, deeply umbilicated, with the aperture lip rising from the left side. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wide anteriorly, narrowing gradually at about $\frac{1}{3}$ of its length, and continuing posteriorly as a narrow canal. Columellar margin thickened. Surface smooth and shiny. Sculpture reduced to fine growth lines, except for the areas near the anterior and posterior ends of the shell, with several conspicuous spiral lines. Color reddish brown, scattered with irregular white and black blotches. Columella white.

EXTERNAL MORPHOLOGY.—Body is oval, 9 mm long in the largest specimen examined. Cephalic shield short, comprising about $\frac{1}{4}$ of the body length (Fig. 7B). Each side of the head with an involute lateral extension. Hancock's organs composed of 7 simple folds. Posterior $\frac{5}{8}$ of the body almost entirely covered by the shell. Gill simple, composed of 15 unipinnate lamellae. Color of the living animals pale brown, with numerous small white spots. Shell completely opaque.

ANATOMY.—Buccal bulb oval to elongate, connected posteriorly to the short esophagus and the long salivary glands (Fig. 11A). Esophagus opening into a large gizzard, which contains three smooth and irregular gizzard plates (Fig. 10F), all of them similar in shape and size. Plates conical, with four ridges and

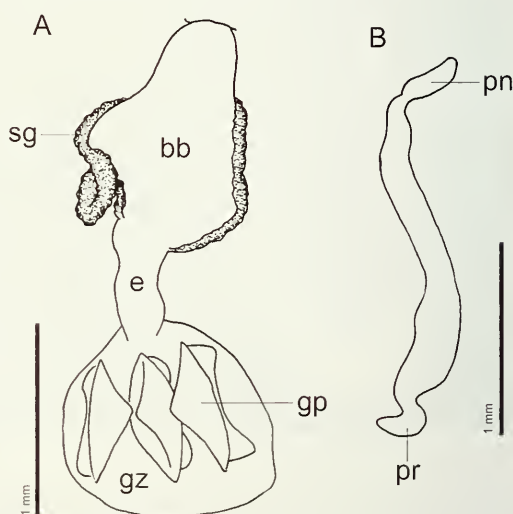


FIGURE 11. *Bulla punctulata* A. Adams in Sowerby, 1850, anatomy of specimen from Isla Bolaños and Playa Coyotera (INB0003502783); (A) Anterior portion of the digestive system; (B) Male reproductive system. Abbreviations: bb, buccal bulb; e, esophagus; gp, gizzard plate; gz, gizzard; pn, penis; pr, prostate; sg, salivary gland.

longitudinal striations on the inner side. Radular formula $21 \times 2.1.2$ in a specimen from Bahía de Salinas (INB0003502783). Lateral teeth wide, with a short base and 5 sharp cusps (Fig. 10G). Rachidian teeth broad, short, with a small, triangular central cusp and four larger denticles on each side of the cusp.

Reproductive system monoaulic. Penis small, connecting to the prostate through a long and convoluted duct (Fig. 11B).

GEOGRAPHIC RANGE.— Reported in the eastern Pacific from Peru to Baja California, Mexico (Skoglund 2002).

REMARKS.— The specimens here examined have similar shell morphology to the two syntypes of *Bulla punctulata* and there is no doubt they belong to the same species.

Family Aglajidae Pilsbry, 1895

Genus *Aglaja* Renier, 1807

Aglaja regiscorona Bertsch, 1972

(Fig. 12A–B)

Aglaja regiscorona Bertsch, 1972:103–104, fig 1.

TYPE MATERIAL.— *Aglaja regiscorona*: HOLOTYPE: Bahía Las Cruces, Baja California del Sur, México (CASIZ 024043); PARATYPES: Bahía Las Cruces, Baja California del Sur, México, three specimens (LACM 1617).

MATERIAL EXAMINED.— San Miguel, Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001498365); SW of Isla Plata, Provincia Guanacaste, 10 m depth, 17 April 2004, 1 specimen, leg. Y. Camacho (INB0003836172).

SHELL MORPHOLOGY.— Length 1 mm; width 0.5 mm in the single specimen examined. Shell calcified with a distinct whorl, a curved apical border, and a broad flat wing (Fig. 12B). Protoconch globose, about 2 whorls, 200 μ m in diameter.

EXTERNAL MORPHOLOGY.— Body elongate, 5 mm long in the specimen examined. Cephalic shield triangular, projecting posteriorly and upwards into a small, three pointed crown (Fig. 12A). Parapodia small, not extending over the dorsal surface. Posterior end of the body with two big lobes lacking a flagellum. Color of the living animal cream white. Dorsum and cephalic shield covered with numerous papillae, speckled with black. Parapodia and posterior lobes with several small black spots.

Geographic range.— Known only from Bahía Las Cruces, Baja California Sur (Skoglund 2002) and Costa Rica (present paper).

Remarks.— *Aglaja regiscorona* was originally described from Baja California based on several specimens collected from Bahía Las Cruces (Bertsch 1972). An examination of the type material has confirmed that the specimen from Costa Rica belongs to the same species. The shell morphology of this species is described here for the first time.

Genus *Navanax* Pilsbry, 1895

Navanax aenigmaticus (Bergh, 1894)

(Fig. 7C)

Navarchus aenigmaticus Bergh, 1894:217, pl. 10, figs. 11–12, pl. 11, figs. 6–9, pl. 12, figs. 8–10.

TYPE MATERIAL.— Untraceable.

MATERIAL EXAMINED.— Bahía Alcyone, Cocos Island, 34 m depth, 25 March 1989, 1 specimen, leg.

K. Kaiser (CASIZ 073370). North side of Isla del Caño (8°43'15"N, 83°53'07"W),

Provincia

Puntarenas, 0 m depth, 18–19 March

1972, 1 specimen, leg. J. McLean

(LACM 72-68.44). Bahía Junquillal,

Sector SE (10°57'55 .2170N,

85°42'07.2810 W), Parque Nacional

Santa Rosa, Provincia Guanacaste, 1

m depth, 9 December 1995, 1 speci-

men, leg. Y. Camacho

(INB0001486933). Playa Grande

(10°20'59.1902N, 85°51'55.8818

W), 500 m W from Punta Carbón,

Provincia Guanacaste, 0 m depth, 11

January 2001, 2 specimens, leg. S.

Avila (INB0003118189). Playa San

Miguel (9°34'45.8380N, 85°08'8

.6800W), Reserva Natural Absoluta

de Cabo Blanco, Provincia Punt

arenas, 2 m depth, 30 April 1995, 1

specimen, leg. G. Mena (INB000

1498434). Playa Manzanillo

(9°56'03.4990N, 84°54'52.7660W),

Isla Golfo de San Lucas, Provincia

Puntarenas, 2 m depth, 9 December

1999, 2 specimens, leg. M. Calderón

(INB0001496008). Estación San

Miguel (9°34'53.9500N, 85°08'28

.5380W), Reserva Natural Absoluta

de Cabo Blanco, Provincia Punt

arenas, 0 m depth, 28 January 1999, 1

specimen, leg. F. Alvarado

(INB0001495820). Punta Uvita

(9°08'44.4580N, 83°45'33.2680W),

Parque Nacional Marino Ballena, Provincia Puntarenas, 0 m depth, 15

January 2000, 2 specimens, leg. M. Calderón (INB0001496175). Punta Uvita (9°08'50.9650N,

83°45'47.1900W), Parque Nacional Marino Ballena, 0 m depth, 13 April 1996, 6 specimens, leg. S. Avila (INB0001486546). East Side of Isla Ballena (9°06'24.5090N, 83°43'35.8230W), Parque Nacional Marino Ballena, Provincia Puntarenas, 6 m depth, 16 January 2000, 1 specimen, leg. M. Calderón (INB0001495898). 500 meters South of Playa Ventanas (9°05'16.1660N, 83°40'50.7600W), Provincia Puntarenas, 0 m depth, 17 January 2000, 1 specimen, leg. M. Calderón (INB0001495974). San Pedrillo (8°36'53.6350N, 83°44'18.3791W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 20 January 2000, 1 specimen, leg. M. Calderón (INB0001495989). San Pedrillo (8°36'40.6143N, 83°44'16.7412W), Provincia Puntarenas, 0 meters depth, 21 January 2000, 1 specimen, leg. M. Calderón (INB0001495985). San Pedrillo (8°37'22.9440N, 83°44'18.3830W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 27 February 1998, 8 specimens, leg. A. Berrocal (INB0001498380). San Pedrillo (8°37'00.1590N, 83°44'11.8370W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 19. 1 specimen, leg. A. Berrocal (INB0001496543). 100 m SE of Punta Curupacha (8°37'57.8040N, 83°13'14.0600W), Provincia Puntarenas, 7 m depth, 29 January 1998, 3 specimens, leg. A. Berrocal (INB0001498379). Roca Negritas (9°12'58.2630N, 83°50'14.2490W), Provincia Puntarenas, 0 m depth, 17 May 1995, 2 specimens, leg. M. Madrigal (INB0001482914). Rock in front Cabo Matapalo (8°22'17.3370N, 83°17'31.7800W), Península de Osa, Provincia Puntarenas, 18 m depth, 13 February 1997, 1 specimen, leg. S. Avila (INB0001498367).

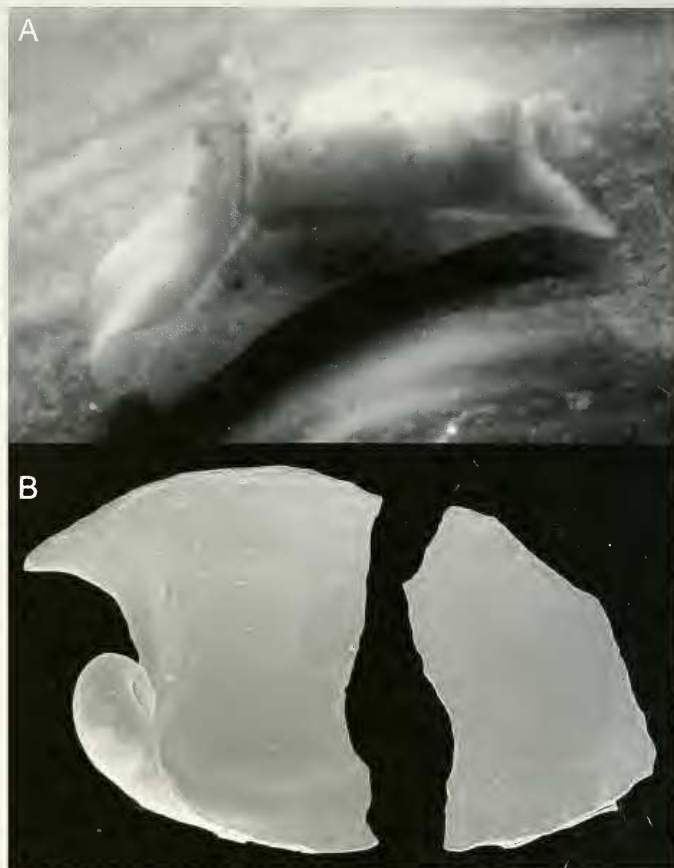


FIGURE 12. *Aglaja regiscorona* Bertsch, 1972, specimen from Cabo Blanco (INB0001498365); (A) Living animal; (B) Shell morphology, 1 mm long (complete).

Cambutal (9°13'21.0780N, 83°50'22.4180W). Provincia Puntarenas, 0 m depth, 16 May 1995, 3 specimens, leg. Y. Camacho (INB0001485355). Punta Voladera, from the tower to NE (8°37'25.8910N, 83°10'56.7300W). Reserva de Vida Silvestre Gelfito, Provincia Puntarenas, 0 m depth, 8 May 1997, 2 specimens, leg. M. Madrigal (INB0001498405). Punta Gallardo (8°37'35.0910N, 83°14'16.2310W). Parque Nacional Piedras Blancas, Puntarenas Provincia, 10 m depth, 6 March 1997, 1 specimen, leg. S. Avila (INB0001498361).

EXTERNAL MORPHOLOGY.— The body is very elongate, 30 mm long, in the specimens examined. The cephalic shield is also elongate, comprising about $\frac{1}{2}$ of the body length (Fig. 7C). The two Hancock's organs are composed of about 16 simple folds. There are large sensory processes at each side of the mouth opening. The parapodia are narrow. The posterior shield is rounded posteriorly, with two broad lobes similar in size and shape. The gill is simple, with 11 groups of lamellae. The color of the living animals is pale brown with irregular large brown spots that vary in position and size. There is a series of bright blue spots on each side of the head and along the edge of the parapodia.

GEOGRAPHIC RANGE.— Widespread in the tropical and subtropical eastern Pacific and Atlantic. In the Pacific it ranges from Southern Mexico to Chile (Skoglund 2002).

REMARKS.— The systematics of *Navanax aenigmaticus* has been investigated by Gosliner (1980), who provided a complete list of synonyms. Gosliner (1980) also provided illustrations of the anatomy and shell morphology of the species, so that information is not repeated here.

Navanax polyalphos (Gosliner and Williams, 1972)

(Figure 13A–C)

Chelidonura polyalphos Gosliner and Williams, 1972:424–436.

TYPE MATERIAL.— *Chelidonura polyalphos*: HOLOTYPE: Bahía San Carlos, 6 km north of Guaymas, Sonora, México (CASIZ 549).

MATERIAL EXAMINED.— 500 m W of Punta Carbón, Playa Grande, Provincia Guanacaste, 0 m depth, January 11, 2001, 1 specimen, leg. S. Avila (INB0003118180); South side of Punta Zapotal, Provincia Guanacaste, 8–10 m depth, April 15, 2004, 1 specimen, leg. T.M. Gosliner (INB0003836138).

SHELL MORPHOLOGY.— Length 2.5 mm; width 1.25 mm, in the single specimen examined. Shell calcified with a distinct wing-like structure protruding from the body whorl. The inner edge of the wing is thickened (Fig. 13). The protoconch is globose, about 1.5 whorl, 200 μ m in diameter. Color yellowish brown.

EXTERNAL MORPHOLOGY.— The body is elongate, 5–20 mm long, in the specimens examined. The anterior end of the body has two grooved lobes. The eyes are large and are visible on the dorsal surface of the cephalic shield. The posterior end of the body terminates in two long acute "tails." The cephalic shield covers the anterior and pharyngeal region of the animal while the posterior shield covers the mantle and posterior viscera. The color of the living animals is dark brown, almost black, and generally with two rows of bright blue spots near the inner side of the parapodia. There are numerous small whitish spots, larger and more numerous in some areas of the dorsal surface. Often, these spots are aggregated to form patches on the shields. In some specimens there are also some small yellowish spots.

GEOGRAPHIC RANGE.— Known from the Channel Islands in southern California to Panama.

REMARKS.— Gosliner and Williams (1972) provided a complete description of this species including illustrations of the reproductive and nervous system and shell morphology of the species, so that information is not repeated here.

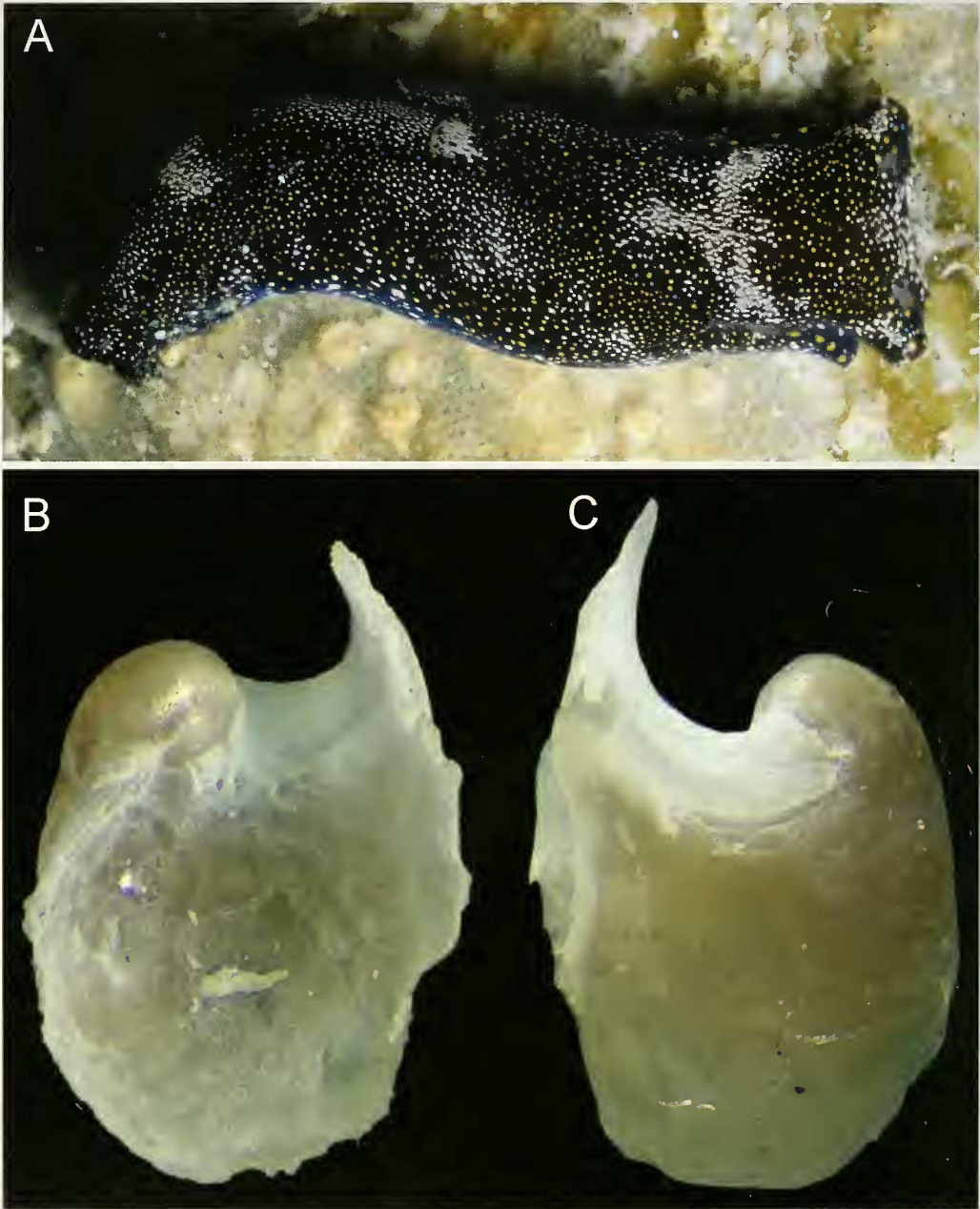


FIGURE 13. *Navanax polyalphos* Gosliner and Williams, 1972, specimen from Guanacaste (A) Living animal, (B) Detail of the ventral side of the shell, 2.5 mm long, (C) Detail of the dorsal side of the shell, 2.5 mm long.

ACKNOWLEDGMENTS

The authors would like to recognize the generous help of several individuals and institutions. Most of the material deposited at INBio was collected by F. Alvarado, R. Angulo, S. Avila, A. Berrocal, M. Calderón, C. Cano, J. Espinosa, M. Lobo, M. Madrigal, G. Mena, and F. González. Most specimens deposited at LACM were collected by D. Cadien, P. LaFollete, and J. McLean. Maribel Zúniga took photographs of the shells, and Terry M. Gosliner and Leopoldo Moro took photographs of the living animals. Lindsey Groves curated the LACM material and made constructive comments on the manuscript.

Fieldwork in Costa Rica by INBio was funded by the Instituto Nacional de Biodiversidad (INBio) through the Netherlands' Government project "Development of biodiversity knowledge and sustainable use in Costa Rica."

The SEM work was conducted at the LACM facility supported by the National Science Foundation MRI grant DBI-0216506.

REFERENCES

- ADAMS, C.B. 1852. *Catalogue of Shells Collected at Panama, with Notes on their Synonymy, Station, and Geographical Distribution*. Craighead, New York. viii + [5]–334 pp.
- BAKER, F., AND G.D. HANNA. 1927. Expedition of the California Academy of Sciences to the Gulf of California in 1921. *Proceedings of the California Academy of Sciences* 16:123–135, pl. 4.
- BEHRENS, D.W. 1991. *Pacific Coast Nudibranchs: a Guide to the Opisthobranchs, Alaska to Baja California*. Second Edition. Sea Challengers, Monterey, California. 107 pp.
- BERGH, R. 1894. XIII. Die Opisthobranchen. Reports of the dredging operations off the West coast of Central America to the Galapagos, to the West coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoölogy* 25:125–233, pls. 1–12.
- BERTSCH, H. 1972. Two additions to the opisthobranch fauna of the southern Gulf of California. *The Veliger* 15:103–106.
- BERTSCH, H. 1978. The Chromodoridinae nudibranchs from the Pacific coast of America. Part II. The genus *Chromodoris*. *The Veliger* 20:307–327.
- BERTSCH, H. 1980. A new species of *Bornella* from tropical West-America. *Spixiana* 3:33–42.
- BERTSCH, H., AND A. KERSTITCH. 1984. Distribution and radular morphology of various nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California, México. *The Veliger* 26:264–273.
- BERTSCH, H., A.J. FERREIRA, W.M. FARMER, AND T. L. HAYES. 1973. The genera *Chromodoris* and *Felimida* (Nudibranchia: Gastropoda) in tropical west America: Distributional data, description of a new species, and scanning electron microscopic studies of radula. *The Veliger* 15:287–294.
- BOUCHET, P. 1975. Opisthobranches de profondeur de l'Océan Atlantique. I. Cephalaspidea. *Cahiers de Biologie Marine* 16:317–365 + pls 1–4.
- CARPENTER, P.P. 1857. *Catalogue of the collection of Mazatlan shells in the British Museum. Collected by Frederick Reigen, described by Philip P. Carpenter*. British Museum, London. iv + [ix]–xvi + 552 pp.
- CARPENTER, P.P. 1864. Diagnoses of new forms of mollusks collected at Cape St. Lucas by Mr. J. Xantus. *Annals and Magazine of Natural History*, ser. 3, 13:311–315.
- DALL, W.H. 1871. Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology* 7:93–160, pls. 13–16.
- DALL, W.H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. XXXVIII. Reports on the scientific results of the expedition to the eastern tropical Pacific,

- in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and the Brachiopoda. *Bulletin of the Museum of Comparative Zoölogy* 43:205-487 + pls 1-22.
- DALL, W.H. 1919. Descriptions of new species of Mollusca from the north Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum* 56:293-371.
- ESPINOSA, J., AND J. ORTEA. 2001. Moluscos del Mar Caribe de Costa Rica: desde Cahuita hasta Gandoca. *Avicennia* suplemento 4:1-77.
- FERREIRA, A.J., AND H. BERTSCH. 1975. Anatomical and distributional observations of some opisthobranchs from the Panamic faunal province. *The Veliger* 17:323-330.
- GOSLINER, T.M. 1979. A review of the systematics of *Cylichnella* Gabb (Opisthobranchia: Scaphandridae). *The Nautilus* 93:85-92.
- GOSLINER, T.M. 1980. Systematics and phylogeny of the Aglajidae (Opisthobranchia: Mollusca). *Zoological Journal of the Linnean Society* 68:325-360.
- GOSLINER, T.M. 1996. Opisthobranchia. Pages 1-52 in F.G. Hochberg and P. Scott, eds., *Taxonomic Atlas of the Santa Maria Basin*. Volume 8. *Mollusca*. Santa Barbara Museum of Natural History, Santa Barbara, California.
- GOSLINER, T.M., AND G.C. WILLIAMS. 1972. A new species of *Chelidonura* from Bahía San Carlos, Gulf of California, with a synonymy of the family Aglajidae. *The Veliger* 14:424-436.
- HERTLEIN, L.G., AND A.M. STRONG. 1951. Eastern Pacific expeditions of the New York Zoological Society. XLIII. Mollusks from the west coast of Mexico and Central America. Part X. *Zoologica* 36:67-120, pls. 1-11.
- HINDS, R.B. 1844. *The zoology of the voyage of H. M. S. Sulphur, under the command of Captain Sir Edward Belcher during the years 1836-42. Published under the authority of the lords commissioners of the Admiralty. Edited and superintended by Richard Brinsley Hinds*. Volume 2. *Mollusca*. Smith, Elder & co., London. 72 + iv pp.
- HOUBRICK, J. 1968. A survey of the litoral marine molluscs of the Caribbean coast of Costa Rica. *The Veliger* 11:4-23.
- HOISÆTER, T. 1998. Preliminary check-list of the marine, shelled gastropods (Mollusca) of Golfo Dulce, on the Pacific coast of Costa Rica. *Revista de Biología Tropical* 46(Suplemento):263-270.
- KEEN, A.M. 1971. *Sea shells of tropical West America. Marine mollusks from Baja California to Peru*. Second Edition. Stanford University Press, Stanford, California.
- MARCUS, EV. 1972. On some Acteonidae (Gastropoda, Opisthobranchia). *Papéis Avulsos de Zoologia* 25:167-188, 1 pl.
- MARCUS, EV. 1977. On the genus *Tornatina* and related forms. *Journal of Molluscan Studies* supplement 2:1-35.
- MIKKELSEN, P.M. 1996. The evolutionary relationships of Cephalaspidea s.l. (Gastropoda: Opisthobranchia): a phylogenetic analysis. *Malacologia* 37:375-442.
- MIKKELSEN, P.S., AND P.M. MIKKELSEN. 1984. Comparison of *Acteocina canaliculata* (Say, 1826), *A. candeï* (d'Orbigny, 1841), and *A. atrata* spec. nov. (Gastropoda: Cephalaspidea). *The Veliger* 27:164-192.
- ORBIGNY, A. d'. 1835-1843. *Voyage dans l'Amérique Méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, La Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833*. Volume 5. Partie 3: Mollusques. Bertrand, Paris. [Dates of publication: pp. 1-48 (1835), pp. 49-184 (1836), pp. 185-376 (1837), pp. 377-408 (1840), pp. 409-488 (1841), pp. 489-758 + pls 1-85 (1846)].
- ORTEA, J.A., AND E. M. LLERA. 1981. Un nuevo dórido (Mollusca: Nudibranchia) de la Isla Isabel, Nayarit, México. *Iberus* 1:47-52.
- PALMER, K.V. 1958. Type specimens of marine Mollusca described by P.P. Carpenter from the West Coast (San Diego to British Columbia). *Memoirs of the Geological Society of America* 76:1-376.
- PEASE, W.H. 1868. Descriptions of marine Gasteropodae, inhabiting Polynesia. *American Journal of Conchology* 4:71-80, pls. 7-10.
- ROBINSON, D., AND M. MONTÓYA. 1987. Los moluscos marinos de la costa Atlántica de Costa Rica. *Revista de Biología Tropical* 35:375-400.

- RUDMAN, W.B. 1971. The family Acteonidae (Opisthobranchia, Gastropoda) in New Zealand. *Journal of the Malacological Society of Australia* 2:205–214.
- SKOGLUND, C. 2002. Panamic Province molluscan literature. Additions and changes from 1971 through 2001. III Gastropoda. *The Festivus* 23(supplement):i–xi, 1–286.
- SOWERBY, G.B. 1848–50. *Thesaurus Conchyliorum, or Monographs of Genera of Shells*. Volume 2. Sowerby, London. [Dates of publication: pp. 493–505, pls 92–108 (1848), pp. 507–552, pls 109–118bis (1849), pp. 553–899, pls 119–186 (1850)].
- SPHON, G.C., AND D.K. MULLINER. 1972. A preliminary list of known opisthobranchs from the Galapagos Islands collected by the Ameripagos Expedition. *The Veliger* 15:147–152.
- STEARNS, R.E.C. 1897. Description of a new species of *Actaeon* from the Quaternary bluffs at Spanish Bight, San Diego, California. *Proceedings of the United States National Museum* 21:297–299.
- STRONG, A.M., AND L.G. HERTLEIN. 1937. The Templeton Crocker Expedition of the California Academy of Sciences, 1932, No. 35. *Proceedings of the California Academy of Sciences* 22:159–178, pls. 34–35.
- STRONG, A.M., AND L.G. HERTLEIN. 1939. Marine mollusks from Panama collected by the Allan Hancock Expedition to the Galapagos Islands, 1931–1932. *The Allan Hancock Pacific Expeditions* 2:177–245.
- THOMPSON, T.E. 1976. *Biology of opisthobranch molluscs*. Volume 1. The Ray Society, London. 206 pp.
- WILLETT, G. 1944. New species of mollusks from Redondo, California. *Bulletin of the Southern California Academy of Sciences* 43: 71–73.